

REVIEW OF THE FAMILY PLEUROBRANCHAEIDAE (MOLLUSCA, OPISTHOBRANCHIA)

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(With 25 figures)

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ABSTRACT

A review of the Pleurobranchaeidae is provided, including keys to the notaspidean genera and the described species of Pleurobranchaeidae. Eleven members of the family are considered as junior synonyms while eight additional species are insufficiently described and their status remains uncertain. The morphology of eleven previously described and six new species is characterized and discussed. New taxa are *Pleurobranchaea (Macfarlandaea)* subgen. nov., and *Pleurobranchaea confusa*, *P. augusta*, *P. bonnieae*, *P. bubala*, *P. notmec*, and *P. vayssierei* spp. nov.

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INTRODUCTION

This paper was originally intended to be the eighth contribution to the catalogue of the western Atlantic warm-water Opisthobranchia (Marcus, Ev. 1972a, 1972b, 1973, 1974, 1978, 1980, 1982a). During the course of investigations it was

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determined that the family Pleurobranchaeidae was in need of substantial revision and the scope of this work was expanded.

The classification of the Pleurobranchaeidae has in many cases been based upon insufficiently described material, and the species were often simply identified with previous descriptions from geographically related regions. Vayssière (1885: 108) found that the descriptions and diagnoses of the Pleurobranchacea had been so incomplete that the species were confused, considered as synonyms, or recorded only as varieties. He tried to define clearly the important characters.

The external morphology is influenced by preservation, contraction, and loss of pigment. The presence of well-separated rhinophores serves as a familial distinction.

The jaw plates and radula can be used for generic separation but hardly differ within a genus. Vayssière (1901: 72) maintained that jaws and radula are indispensable for classification. He stated that it was a pity that Bergh had not figured jaws and radula, as the comparison of these organs might have eliminated all doubts (Vayssière 1901: 51, 71).

Few authors have described the reproductive organs completely, although these offer good specific characters (Vayssière 1901: 53). This is probably largely due to the fact that the reproductive organs are very difficult to dissect without tearing the various ducts, as indicated by Vayssière (1901: 38). For this study there are sufficient specimens of some species, but in the case of several others complete descriptions cannot be given nor can all specimens be classified. Often the male organs have not been observed in detail and they are often species-specific in their structure. For these reasons the present authors have concentrated on the determination of penial morphology but describe other characters whenever possible.

Vayssière (1898: 234) described the oviduct entering the albumen gland in the Berthellinae: *Berthellina brocki* (fig. 180) and *Berthella ocellata* (fig. 182). In *Berthellina edwardsi* (fig. 179) the duct, though touching the albumen gland, seems to continue (p. 234) to its own outer opening. Vayssière stated that in the Pleurobranchidae, *Pleurobranchus* (figs 177–178), *Susania*, and *Oscanius*, and in the Pleurobranchaeidae there is no such connection; the oviduct goes directly into the vagina and the gland mass opens into the outer part of the vagina. In earlier papers the senior author also misinterpreted the close proximity of the oviduct to the gland mass as an entrance in *Pleurobranchus aerolatus* (Marcus, Ev. & Marcus 1967a: 165, fig. 19, o), *Pleurobranchaea gela* (Marcus, Ev. & Marcus 1966: 176, fig. 37, oi), and *P. agassizii* (Marcus, Ev. & Marcus 1967a: 49, fig. 56D, ov).

GENERAL CHARACTERS OF THE PLEUROBRANCHAEIDAE

The colours are variable in life, but most species are brownish. A shell is absent. The size differs between species but depends on age and may vary between populations. The notum varies in size. It is usually slightly smaller than or

equal to the foot in size, but sometimes it is larger. The relative proportions of the mantle to the foot were used for generic separation but they are largely dependent upon the degree of contraction during preservation. Anteriorly the notum is separated from the oral veil by a slight fold. The notum may be smooth or rough, or with bosses or tubercles, which may be altered during preservation.

The right side of the notum projects over the gill, forming an exhalant siphon posteriorly. On the left side the notum sometimes leaves the upper side of the foot free. Posteriorly it merges gradually with the upper side of the foot. In *Pleurobranchaea brockii* the notum and foot remain separated posteriorly.

The oral veil is broad. Its anterior border bears one or two rows of simple or branched papillae, which may disappear with fixation. The sides of the veil form the oral tentacles, which are split posteriorly and inwardly rolled. The blunt, rolled rhinophores are situated in the angles between the tentacles and lateral notal borders and are well separated from each other.

Between the right rhinophore and the gill are the genital apertures, surrounded by a circular fold. This fold often has one or two flaps that are frequently protruded. The flaps vary intraspecifically. Behind these apertures lies the prebranchial gland, Bourne's gland, called the organ of Bojanus by Moquin-Tandon (1870: 20). It opens on a small papilla.

The gill occupies the middle of the right side below the border of the notum. It has a variable number of pinnae on both sides, which increases with age. The gill rachis is smooth or bears two rows of papillae, which may disappear with preservation. Part of the underside of the gill is adnate to the body wall. The anal opening is situated between the gill and notum, while the nephropore is ventral to the gill.

The anterior border of the foot is transversely grooved. The hind end is rounded and often bears a soft spur or horn on the dorsal side. The presence or absence of the spur (Figs 6A, 13A) varies intraspecifically. The pedal (metapodial) gland on the ventral side of the foot is not always visible. Macnae (1962: 168-169) found this gland only in sexually active individuals, although its absence may be a result of poor preservation.

The mouth opening is often extended by the everted buccal cavity and protruded pharynx. The pharynx has a vertical entrance to the digestive tract and is flanked by the jaw plates. The anterior border of the jaws may vary in shape (Figs 6G, 19C) even in the same species (Marcus, Ev. & Marcus 1966, fig. 35). The platelets comprising the jaws are polygonal columns with a flat surface. The ratio of length to breadth of the platelets varies intraspecifically and may vary with position in a single individual (Fig. 10C-F). We agree with O'Donoghue (1929: 58) that the jaw platelets cannot be utilized for specific separation.

The radula has numerous transverse rows of uncinat, uni- or bicuspid teeth. A rachidian tooth is rarely present. The teeth are largest in the middle of the half-row. The presence or absence of a secondary denticle on the teeth is variable. The number of unicuspid teeth on the outer edge of the radula also varies. In some specimens of *P. tarda* there are up to twenty unicuspid teeth,

while in other individuals they are entirely absent. We believe that the rudimentary secondary cusp on all teeth in *P. californica* is a useful subgeneric character. In specimens where the radular rachis is more or less complete, the first lateral tooth varies in size in different rows. It gradually increases in size from older teeth to newer and ranges from 0,105 to 0,250 mm. As additional teeth are added to the radula from the inner side, the size of the inner lateral again decreases. Malformations of teeth are not rare. Most commonly two adjacent teeth are fused within a transverse row. On one occasion two entire transverse rows of abnormal teeth were observed (Fig. 13B).

The stomach often contains the remains of food, demonstrating the variability of diet within the Pleurobranchaeidae. In the specimens examined, prey included the bryozoan *Cellaria* sp., polychaetes up to 15 mm long, an amphipod, a small prosobranch shell, a specimen and a pharynx of a pleurobranchid, a gymnosomatid radula, an aeolid 2,5 mm long and a complete pharynx with jaw plates and radula, a 20 mm branch of a crinoid, a spine of the sea urchin *Eucidaris tubulinoides* (identified by F. M. Bayer, U.S. National Museum) and a 6 mm long octopod. A 65 mm specimen of *Pleurobranchaea brockii* contained four specimens of *Philine aperta* in its stomach, the largest of which was 18 mm in length. Eales (1937) found fourteen specimens (10–17 mm long) of *Pleurobranchaea tarda* in the stomach of *Pleurobranchella nicobarica*.

Bergh (1897: 2) indicated that a blood gland is situated dorsal to the heart in the Pleurobranchacea, not over the central nervous system as in the Doridacea.

Bergh's (1897: 25–26, pl. 4 (figs 1–7)) description and figures of the cuticular penial tube of *P. meckelii* differ from Vayssi re's (1901: 40–41, fig. 228). As this is the evaginable part of the male duct, we consider it as the penis proper. Bergh's (1897: 34–37) terms for the reproductive ducts differ somewhat from ours. Vayssi re (1901: 39–40, pls 4–6) described the male duct of *P. meckelii*. He called Bergh's term 'penial sheath' the penial sac (his fig. 224) and applied the term 'penis' rather than 'glans penis' to the small muscular cone at the opening of the efferent duct into the atrium (his figs 225–226). He did not mention nor figure any cuticularized penis inside the efferent duct, except for a transverse section (fig. 228). Macnae (1962) roughly figured the penis of four pleurobranchid species. MacFarland (1966: 99, pl. 17 (figs 1–7)) described and figured the 'glans penis' of *Pleurobranchaea californica* and compared it with Bergh's description of *P. meckelii*.

The inner genital organs dissected from the intestine and digestive gland, but still connected with the body wall, can best be studied by slightly staining them in carmine and sketching them before clarification to see the cuticular penis, if present. In laying the organs flat (Vayssi re 1901: 38) for balsam preparations they frequently stick together or tear, so that the course of the ducts is no longer recognizable.

From the ovotestis, in which the follicles contain either sperm or oocytes (Mazzarelli 1891: 234), a winding hermaphroditic duct emerges. It widens as an

elongate ampulla. Shortly after it narrows again, it divides into the oviduct and male duct.

The ciliated oviduct widens, forming some pouches full of sperm, the spermatocyst (Fig. 3B, y). The following long, coiled portion is also ciliated. The oviduct enters the vagina near the stalk of the vesicular spermatheca. The albumen and mucous glands open into the vagina.

The male duct generally enters the centre of a round prostatic gland composed of many narrow tubules. It emerges from the gland on the opposite side and enters the penial sac, when present, usually near its fundus and often close to the retractor muscle. In *Euselenops* the prostatic cells are contained with the efferent duct.

The penial sac is narrow along the loop of the efferent duct in *P. tarda* and slightly wider in *P. maculata*, *P. bubala*, and *P. californica*, and widest in *P. meckelii* and *P. augusta*. In one specimen of *P. notmec* and in *P. bonnieae* and *P. inconspicua*, it is tight around the many windings of the efferent duct (Fig. 18F). The number of crowded windings of the efferent duct in the penial sac in *P. inconspicua*, *P. bonnieae* and *P. notmec* could not always be accurately determined. The penis is not known in detail for *P. maculata*. The penis does not have a cuticle in *P. agassizii*, *P. brockii*, *P. bonnieae*, and *P. vayssierei*. It is covered with papillae in *Euselenops luniceps*, and with cuticular hooks in *Pleurobranchella nicobarica* (Fig. 24D) and *Koonsia obesa*. There is an external cuticle in *Pleurobranchaea notmec* (Fig. 18C–E), and an internal cuticular cylindrical stylet of different transverse section (Fig. 1A–H) in *Pleurobranchaea meckelii*, *P. tarda*, *P. inconspicua*, *P. californica*, and *P. bubala*.

The spermatocyst is often a simple widening, or its epithelium forms pouches. In *P. brockii* it is generally a spiral caecum of three to five whorls, but in one specimen (SAM–A29866) it consisted of epithelial pouches.

The spermatheca is small and not transparent, or wide and thin-walled. In *P. bubala* there may be a larger ental vesicle with a smaller ectal one on its top (Fig. 16G).

Mazzarelli (1891: 233–238, figs 1–3) gave an excellent description of the reproductive apparatus of *P. meckelii*, but seemed to have confused the prostate and albumen glands. He described the cuticular tube in the efferent duct, though he called it a filament. By dissecting mating specimens he found that the cuticular tube is projected from the everted penial sheath into the widenings of the inner oviduct of the partner, the spermatheca and spermatocyst.

KEY TO THE NOTASPIDEAN GENERA

- | | | |
|---|--|----------------------|
| 1 | Shell external | 2 |
| — | Shell internal or absent | <i>Gymnotoplax</i> 5 |
| 2 | Shell partly covered by mantle | <i>Gymnotoplax</i> 3 |
| — | Shell not covered by mantle (Umbraculacea) | 3 |
| 3 | Gill from left rhinophore along front and most of right side | <i>Umbraculum</i> |
| — | Gill only on part of the right side | 4 |
| 4 | Rachidian tooth present | <i>Tyrodina</i> |
| — | No rachidian tooth | <i>Roya</i> |

- 5 Shell internal; rhinophores anteromedial, posterior to veil; jaw elements flat posteriorly, pointed anteriorly (Pleurobranchidae) 6
 — Shell absent, rhinophores lateral, between veil and mantle border; jaw elements more or less high polygonal column (Pleurobranchaeidae) 11
 6 Oviduct enters albumen gland (Berthellinae) 7
 — Oviduct unites with vagina (Pleurobranchinae) 9
 7 Teeth lamelliform 8
 — Teeth hook shaped *Berthella*
 8 Teeth with one secondary cusp; prostatic gland cells in male duct *Pleurehdera*
 — Teeth denticulate; prostate present *Berthellina*
 9 Prostate present 10
 — Prostatic gland cells in male duct *Susania*
 10 Shell large; big flaps around genital apertures *Oscanius*
 — Shell small, no big flaps around genital apertures *Pleurobranchus*
 11 Notum half the length of foot 12
 — Notum larger than foot or equal 13
 12 Fold on hind end of notum, penis papillate *Euselenops*
 — Spur on hind end of foot, penis with hooks *Koonsia*
 13 Radular teeth unicuspid *Pleurobranchella*
 — Radular teeth bicuspid 14
 14 Secondary cusp of tooth well developed *Pleurobranchaea* (*Pleurobranchaea*)
 — Secondary cusp rudimentary *Pleurobranchaea* (*Macfarlandaea*)

SPECIES OF THE FAMILY PLEUROBRANCHAEIDAE TREATED IN THE PRESENT PAPER

- Pleurobranchaea meckelii* Leue, 1813; Mediterranean to Gulf of Guinea
P. maculata (Quoy & Gaimard, 1832); Australia, New Zealand, Japan
P. tarda Verrill, 1882: 546; western and south-eastern Atlantic
P. agassizii Bergh, 1897; western Atlantic
P. brockii Bergh, 1897: 41; Japan to South Africa
P. inconspicua Bergh, 1897: 49; western Atlantic, Mediterranean, Israel
P. confusa sp. nov. *pro parte* *Koonsia obesa*, Verrill; north-western Atlantic
P. augusta sp. nov.; west Africa
P. bonnieae sp. nov.; Florida
P. bubala sp. nov.; South Africa
P. notmec sp. nov.; Israel
P. vayssierei sp. nov.; Algiers
P. (Macfarlandaea) subgen. nov.
P. (M.) californica MacFarland, 1966: 94; California
Euselenops luniceps (Cuvier, 1817); Japan to South Africa
Koonsia obesa Verrill, 1882: 545; 1884, pl. 28 (fig. 7); western Atlantic
Pleurobranchella nicobarica Thiele, 1925: 283; Indian Ocean, South Africa
Gigantonotum album Lin Guangyu & Tchang Si, 1965; China

LIST OF SYNONYMS

- Pleurobranchaea meckelii* var. *occidentalis* Bergh, 1897: 28; syn. nov. of *P. tarda*
Pleurobranchaea hedgpethi Abbott, 1952; syn. nov. of *P. inconspicua*
Oscaniopsis semperi Bergh, 1897: 54; syn. of *Euselenops luniceps*
Oscaniopsis compta Bergh, 1897: 58; syn. of *Euselenops luniceps*
Oscaniopsis amboinei Vayssi re, 1901: 15; syn. of *Euselenops luniceps*

- Pleurobranchaea capensis*, Vayssière, 1901: 46; *syn. nov.* of *P. tarda*
Pleurobranchoides gilchristi O'Donoghue, 1929: 62; *syn. nov.* of *Pleurobranchella nicobarica* Thiele
Pleurobranchaea hamwa Marcus & Marcus, 1955: 21; *syn.* of *P. inconspicua*
Pleurobranchaea gemini Macnae, 1962: 178; *syn. nov.* of *P. brockii*
Pleurobranchaea gela Marcus & Marcus, 1966: 174; *syn. nov.* of *P. inconspicua*
Pleurobranchaea occidentalis Bergh, 1897: 28; *syn. nov.* of *P. tarda*
Pleurobranchaea novaezealandiae Cheeseman, 1878: 378; *syn.* of *P. maculata*

INSUFFICIENTLY DESCRIBED SPECIES NOT TREATED HERE

- Pleurobranchillus morosus* Bergh, 1892: 28
Pleurobranchaea morula Bergh, 1905: 48
Pleurobranchaea melanopus Bergh, 1907: 33
Oscaniopsis pleurobranchaeana Bergh, 1907: 35
Pleurobranchaea algoensis Thiele, 1925: 282
Pleurobranchaea japonica Thiele, 1925: 283
Pleurobranchaea dorsalis Allan, 1933: 445

Classification, synonymy, and geographic distribution of the insufficiently described species remain doubtful, particularly as two or more well-distinguished species may be sympatric.

KEY TO THE SPECIES OF THE FAMILY PLEUROBRANCHAEIDAE

- | | | |
|----|---|--|
| 1 | Notum half the length of the foot | 2 |
| — | Notum larger than foot or equal | 3 |
| 2 | Fold on hind end of notum, penis papillate | <i>Euselenops luniceps</i> |
| — | Spur on hind end of foot, penis with hooks | <i>Koonsia obesa</i> |
| 3 | Radular teeth unicuspid | <i>Pleurobranchella nicobarica</i> |
| — | Radular teeth bicuspid | 4 |
| 4 | Secondary cusp of tooth well developed | <i>Pleurobranchaea (Pleurobranchaea)</i> |
| — | Secondary cusp rudimentary | <i>Pleurobranchaea (Macfarlandaea) californica</i> |
| 5 | Penis soft, cuticle absent | 6 |
| — | Penis cuticular | 11 |
| 6 | Vagina short | 7 |
| — | Vagina long | 10 |
| 7 | No penial sac | <i>P. agassizii</i> |
| — | Penial sac developed | 8 |
| 8 | Penial sac narrow | <i>P. maculata</i> |
| — | Penial sac globular | 9 |
| 9 | Root of penis enlarged | <i>P. bonnieae</i> |
| — | Root of penis not wider than following part | <i>P. vayssierei</i> |
| 10 | Penis very long and thick | <i>P. brockii</i> |
| — | Penis short | <i>P. confusa</i> |
| 11 | Penis a slightly curved stylet | 12 |
| — | Penis a long tube with many loops in penial sac | 13 |
| 12 | Penial sac narrow, tubular | <i>P. tarda</i> |
| — | Penial sac widened around duct | <i>P. bubala</i> |
| 13 | Vagina short | 14 |
| — | Vagina long | <i>P. meckelii</i> |
| 14 | Penial cuticle with crest, less than ten loops in penial sac | <i>P. augusta</i> |
| — | Penial cuticle cylindrical, ovoid in transverse section, up to twenty loops in penial sac | <i>P. inconspicua</i> |

Remarks

Sufficient characters were not obtained to include *P. notmec* sp. nov. in the key, though in the discussion it is distinguished from similar species. Bergh's (1892: 27, 28) genus *Pleurobranchillus* for *morosus* and *brockii* was synonymized to *Koonsia* by Pilsbry (1896: 221, 223) and by Abbott (1974: 349). Later Bergh (1897: 27, 28) transferred *morosus* and *brockii* to *Pleurobranchaea*.

Thiele's (1925: 283) *Pleurobranchella* and its synonym *Pleurobranchoides* O'Donoghue, 1929, have a notum noticeably larger than the foot. This is exceptional in the family Pleurobranchaeidae.

Pleurobranchaea Leue, 1813

Pleurobranchidium Blainville, 1824.

Cyanogaster Blainville, 1825.

Pleurobranchillus Bergh, 1892.

Koonsia Verrill, 1882, partim.

Non *Pleurobranchella* Thiele, 1925.

Type species

Pleurobranchaea meckelii Leue, 1813.

Diagnosis

Pleurobranchaeidae with bicuspid radular teeth.

Pleurobranchaea (*Pleurobranchaea*) Leue, 1813*Type species*

Pleurobranchaea meckelii Leue, 1813.

Diagnosis

Secondary cusp of radular teeth well developed.

Remarks

Thiele's (1931: 419) definition is confused and the forms he attributed to the subgenus have quite different characters.

Pleurobranchaea meckelii Leue, 1813

Figs 1A, H-P, 2A-C

Pleurobranchaea meckelii Leue, 1813.

Pleurobranchidium meckelii Blainville, 1824.

Pleurobranchaea meckelii Leue, 1813. Mazarelli, 1891: 223. Pelseneer, 1894: 31, figs 86-99.

Bergh, 1897: 7, pls 1-4, pl. 7 (figs 16-18); 1899: 26; 1902: 228, pl. 9 (figs 1-3). Vayssi re, 1901: 42, figs 205-231.

Non *P. meckelii* var. *occidentalis* Bergh, 1897: 28 (= *P. tarda*).

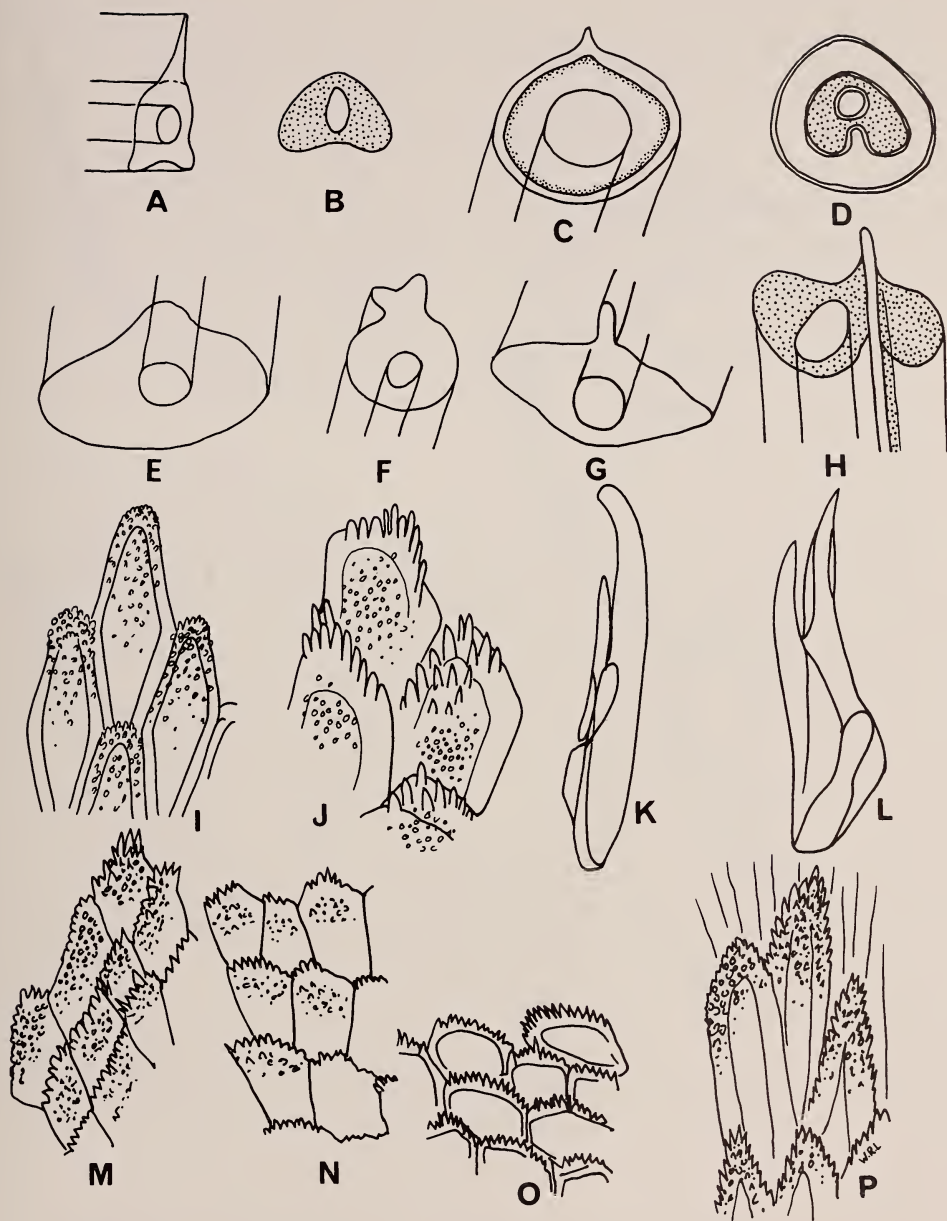


Fig. 1. A-H. Optical transverse sections of penial stylets. A, H. *Pleurobranchaea meckelii* Leue, 1813. B. *P. inconspicua* Bergh, 1897. C. *P. augusta* sp. nov. D. *P. bonnieae* sp. nov. E-G. *P. notmec* sp. nov. I-P. *P. meckelii* Leue, 1813. I-J. Jaw platelets from Vayssière's collection. K-L. Teeth from Algiers specimen. M-P. Jaw platelets from Israel specimen.

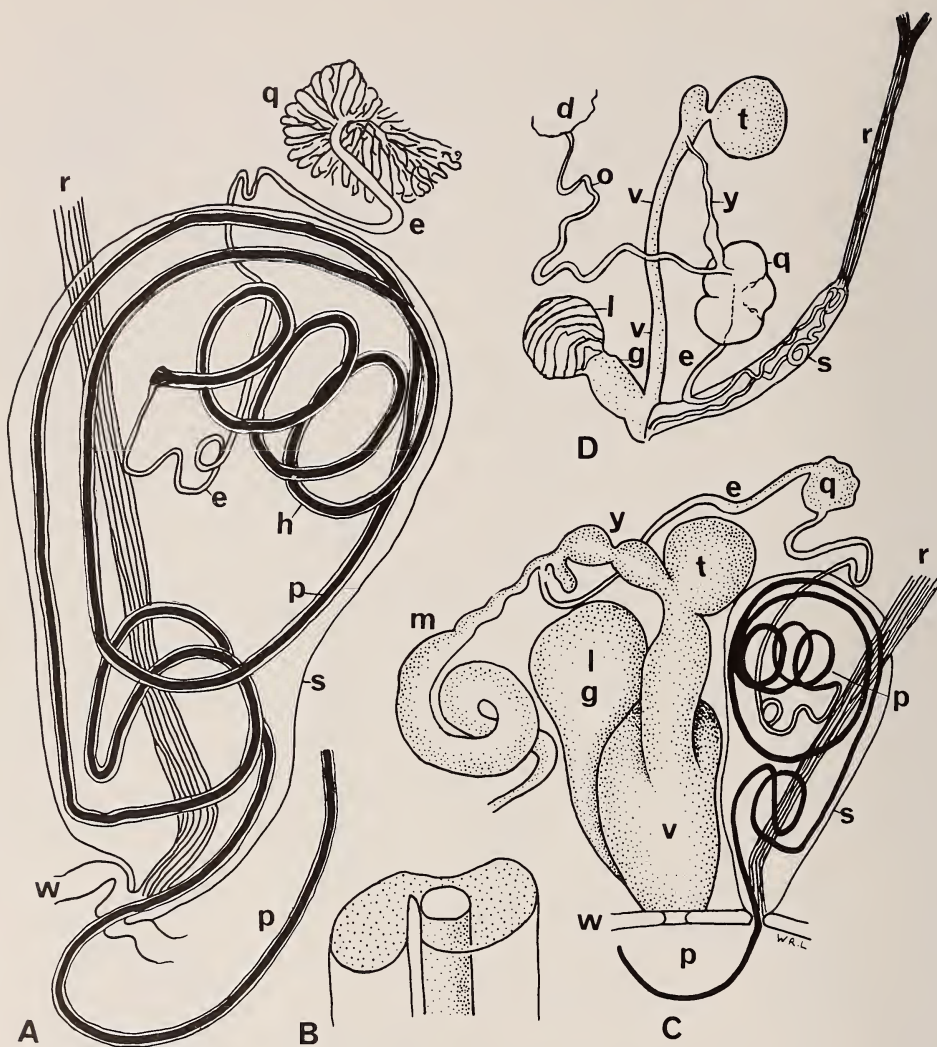


Fig. 2. A-C. *Pleurobranchaea meckelii* Leue, 1813. A. Penial sac. B. Optical section of penial stylet. C. Diagram of reproductive organs. D. *P. maculata* (Quoy & Gaimard, 1832), diagram of reproductive organs (after Vayssi re 1901, fig. 247).

Material

Museum National d'Histoire Naturelle, Paris: two specimens, Algiers, Algeria, 1900; five specimens, Mediterranean, Israel to northern Sinai. Zoology Museum, Copenhagen: some dissected incomplete specimens. United States National Museum, Washington, D.C.: P 239, one specimen, Gulf of Guinea (04 56'N 05 00'E).

Distribution

Mediterranean, Atlantic, Azores (Bergh, 1899); Cape Verde Islands (Vayssière, 1902).

Description

Length up to 100 mm. Radular teeth bicuspid, one to five outermost teeth unicuspid. The efferent duct passes transversely through the retractor muscle. In the strongly muscular penial sac it divides into penis proper and penis sheath. The penis is an elastic cuticular stylet, 0,06–0,1 mm diameter, with a high crest (Fig. 1A, H). It forms no more than six to ten loops and is up to 10,5 mm long.

Vayssière's (1901, fig. 223) figure of the structure of the penis, seen by transparence, evidently refers to a young specimen.

Discussion

Bergh's (1897) and Vayssière's (1901) descriptions and figures of *P. meckelii* differ. Vayssière evidently did not have homogeneous material. He indicated a thin, transparent penial sac in *P. meckelii*, but for one of his samples an opaque, nacraeous, muscular one is present. He did not see the elastic cuticular stylet that we found in his Algerian specimen (Fig. 2B) and in the Israeli specimen (Fig. 1A, H). The latter agrees perfectly with Bergh's description and figure (pl. 4, fig. 4) of the penial stylet, while the present specimen from Algiers has a different transverse optical section.

Vayssière (1901: 43) indicated that *P. meckelii* was the only species occurring in the Mediterranean. Therefore, all subsequent findings of Pleurobranchaeidae from the region were identified as *P. meckelii*. However, the present material from Turkey, Israel, and Algeria contains several other species. Even among the three specimens received from the Museum National d'Histoire Naturelle, of Vayssière's material collected in Algiers in 1890, there was one different from *P. meckelii*. It is called here *P. vayssierei* (see p. 38). The specimen from the Gulf of Guinea extends the range of the species. Most of the synonyms assigned to *P. meckelii* are insufficiently described. This is true of Sturany's (1904) description, and the record of specimens from the Red Sea is questionable (Pruvot-Fol 1933: 91). *P. meckelii* var. *occidentalis* Bergh (1897: 28) is actually *P. tarda*.

Pleurobranchaea maculata (Quoy & Gaimard, 1832)

Figs 2D, 25E

Pleurobranchidium maculatum Quoy & Gaimard, 1832: 301–302, pl. 22 (figs 11–14).

Pleurobranchaea maculata (Quoy & Gaimard, 1832) Vayssière, 1901: 49–56, figs 238–247.

Pleurobranchaea novaezealandiae Cheeseman, 1878: 378. Willan, 1983: 254, figs 57–70.

Distribution

Australia, China, Japan, New Zealand, Sri Lanka.

Description

The length is up to about 50 mm.

The radular formula is $40-49 \times 80.0.80$; ten to fifteen of the outermost teeth lack a secondary denticle.

The reproductive organs described by Vayssi re (1901) differ from those of the other now known species by the long vagina ending in a globular caecum to which the spermatheca is connected (Fig. 2D). The efferent duct winding up and down the retractor muscle in the penial sac is similar to that of *P. tarda* (Fig. 5B), but it evidently does not have a stylet.

Discussion

Vayssi re (1901: 51) studied specimens of Quoy & Gaimard's (1832) original material and found that Bergh's (1898b: 429, pl. 29, figs 2-9) animals from Juan Fernandez were not *P. maculata*. The same must evidently hold for Odhner's (1921: 224) undescribed specimens from Masatierra.

The reproductive organs of a young specimen of *P. tarda* were somewhat similar to those of *P. maculata* in Vayssi re's figure, but the spermatocyst and spermatheca are quite different.

The synonymizing of insufficiently described species only because they also come from the Indo-Pacific region (Thompson 1970) cannot be maintained. *P. melanopus* Bergh (1907: 33), *P. japonica* Thiele (1925: 283), and *P. dorsalis* Allan (1933: 445) are possibly synonyms, but *P. tarda* (Fig. 5) is quite distinct from *P. maculata*. *Pleurobranchoides gilchristi* O'Donoghue (1929: 62), a synonym of *Pleurobranchella nicobarica* Thiele (1925: 283), is a species with unicuspid teeth and is also very different from *P. maculata*.

The male organ of Vayssi re's (1901: 49-56, figs 238-247) *P. maculata* (Quoy & Gaimard, 1832) from Australia is similar to that of Bergh's (1897, pl. 7, fig. 14) *P. tarda*, but it does not have a stylet.

Pleurobranchaea confusa sp. nov.

Fig. 3

Koonsia obesa Verrill, 1882: 545-546, *partim*. Verrill, 1884: pl. 28 (fig. 7). Verrill, 1885, *partim*. *Pleurobranchaea obesa* Bergh, 1897, *non* Verrill: 30-33, pl. 7 (figs 19-21). Vayssi re, 1901, *non* Verrill.

Type material

Holotype: United States National Museum 784657, off Delaware Bay (38 35'N 73 13'W), 400 m, 10 October 1881. This specimen was previously a paratype of *Koonsia obesa*.

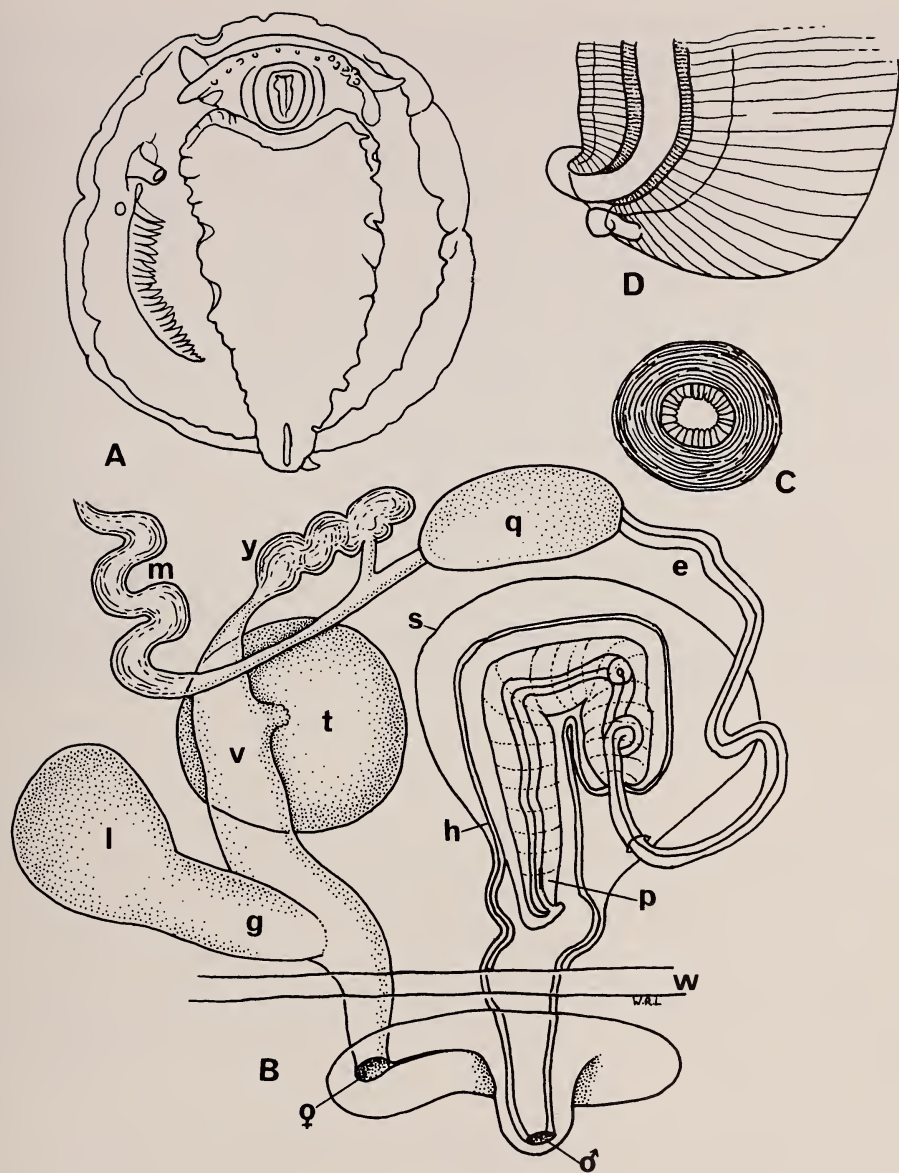


Fig. 3. *Pleurobranchaea confusa* sp. nov. A. Ventral view of preserved specimen (paratype of *Koonsia obesa*). B. Diagram of reproductive organs. C. Optical section of efferent duct in penis. D. Tip of penis.

Further distribution

? Off Martha's Vineyard, Massachusetts.

Etymology

The epithet *confusa* (from Latin: *confusio*) refers to the combination of two distinct species in the original description of *Koonsia obesa*.

Description

The present contracted animal is 4.5 by 4.0 cm and has a smooth, swollen notum extending far out over the foot (Fig. 3A). The oral veil has a single row of papillae. The tentacles and rhinophores are smooth. The triangular foot is narrower and shorter than the notum. It has a broad anterior border, a dorsal spur, and a ventral foot gland (Fig. 3A). The gill has about twenty-six pinnae and a smooth rachis.

The denticles on the jaw platelets are irregular in presence and in size; there are two to twelve denticles per platelet. The radular formula is $34 \times 90.0.90$. Approximately fifteen of the outermost teeth of each row are unicuspid. There is no rachidian tooth.

The male duct enters the prostate and, after leaving it, winds to enter the wide penial sac. Inside the sac it forms a wide sheath and a strongly muscular penis with two tiny cuticular bulbs at its tip (Fig. 3D). The oviduct has some epithelial pouches, the spermatocyst. The oviduct widens and receives the large spermatheca. The wide vagina continues, joining with the female gland mass, and opens through the female aperture (Fig. 3B).

Discussion

This description is based on a paratype of *Koonsia obesa* from Verrill's collection and corresponds to the paratype studied by Bergh (1897: 30–33, pl. 7 (figs 19–21)). It differs from Verrill's (1884, 1885) figures by the swollen and overhanging mantle, elongate tail and the absence of 'small hooks on the verge'. Bergh was quite right to transfer this material to *Pleurobranchaea*. However, specimens of the type species of *Koonsia*, *K. obesa* Verrill, 1882, may be found again. The name *Pleurobranchaea confusa* sp. nov. is proposed for the paratype of *Koonsia obesa*.

Pleurobranchaea tarda Verrill, 1880

Figs 4–5

Pleurobranchaea tarda Verrill, 1880: 398; 1882: 546, pl. 58, (fig. 26). Bergh, 1897: 33, pl. 6 (figs 28–31), pl. 7 (figs 1–15). Vayssière, 1901: 57, figs 248–251.

Pleurobranchaea tarda var. Bergh, 1897: 39, pl. 7 (figs 21–27).

Pleurobranchaea meckelii var. *occidentalis* Bergh, 1897: 28. Vayssière, 1901: 46.

Pleurobranchaea occidentalis Bergh, 1897. Marcus & Marcus 1967a: 45.

Pleurobranchaea capensis Vayssière, 1900. Vayssière, 1901: 46, pl. 4 (figs 232–237). O'Donoghue, 1929: 48, figs 52–57. White, 1955: 173, fig. 6.

Pleurobranchaea maculata Thompson, 1970: 192, *partim.*, non Quoy & Gaimard.

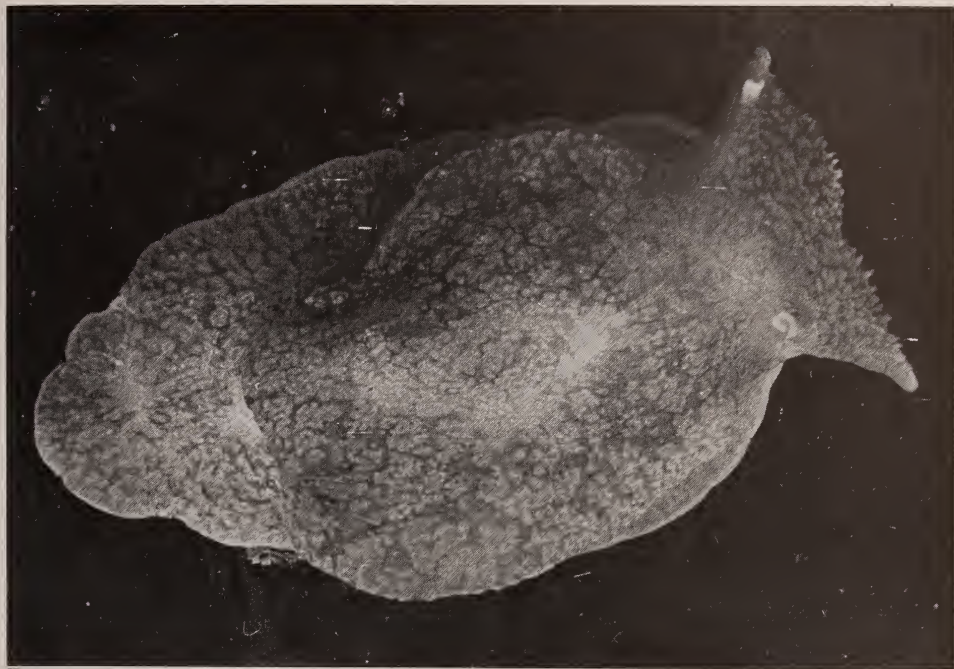


Fig. 4. *Pleurobranchaea tarda* Verrill, 1882, living animal.

Material

About 120 specimens in the U.S. National Museum and South African Museum; western Atlantic, from 31° to 5°N; eastern Atlantic from Ghana and the Cape of Good Hope and False Bay; intertidal to 1 450 m.

Further distribution

From Martha's Vineyard to south of Cuba; Angola and Kabinda; Agulhas Bank (35°10'S 23'E), 500 m.

Description

The present animals preserved, are from 7,5 to 52 mm long. The mantle is generally smooth and about the same size as the foot. On its right side the border often forms an exhalant siphon over the anal opening and the tip of the gill. The tip of the foot often extends posteriorly (Fig. 5C). In some specimens it bears a short spur. The metapodial gland on the end of the sole is rarely developed. The veil, tentacles and rhinophores are typical for the genus. The tubercles of the veil are sometimes preserved. The proboscis is often protracted, and the anterior border of the jaw plates are as variable as in *P. gela* (Marcus, Ev. & Marcus 1966, fig. 35).

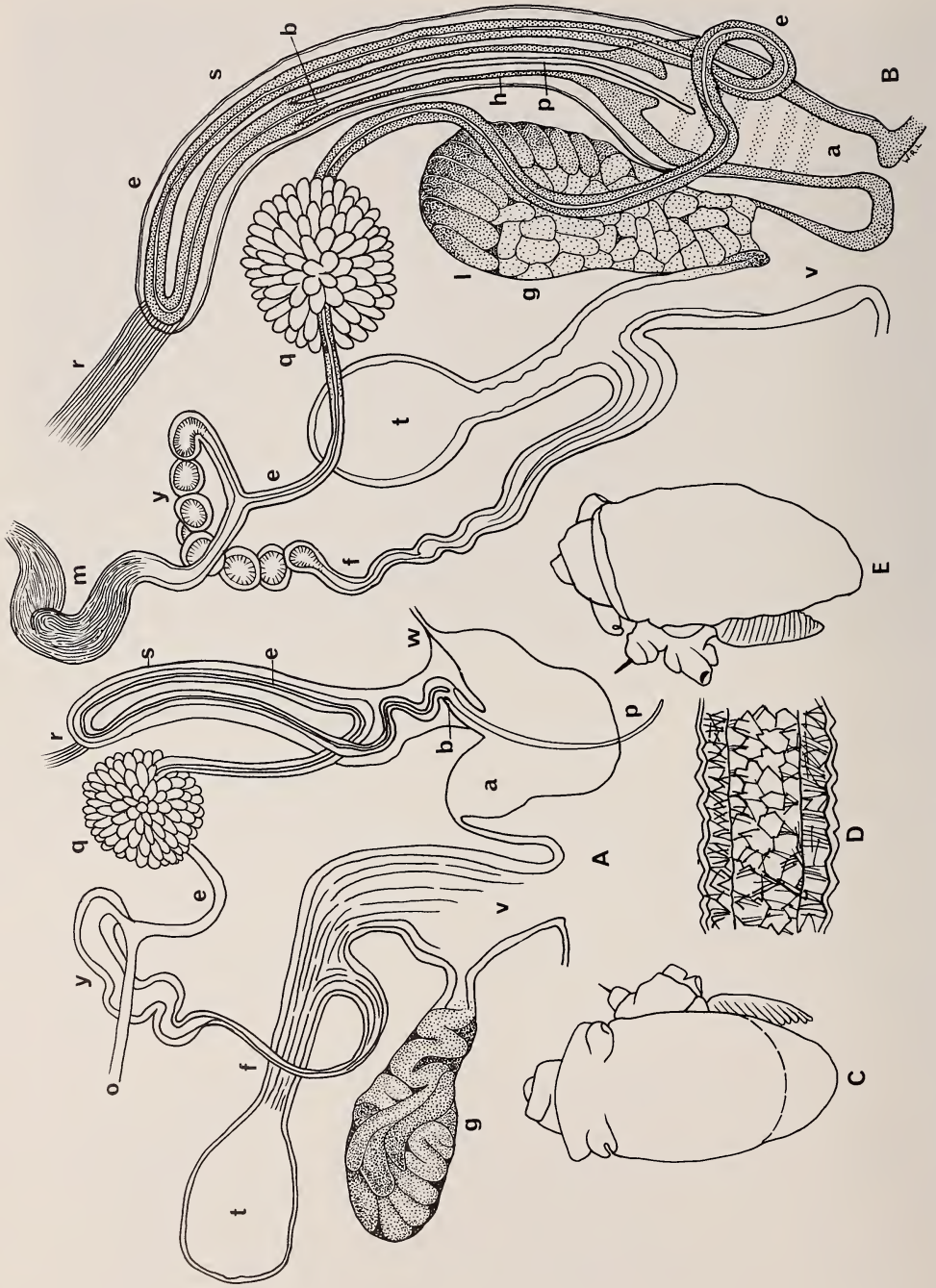


Fig. 5. *Pleurobranchaea tarda* Verrill, 1882. A. Reproductive organs of Nigerian specimen. B. Reproductive organs of western Atlantic specimen. C. Dorsal aspect. D. Part of stylet. E. Ventral aspect.

The gill is adnate for about two-thirds of its length. The anus lies dorsally, just in front of the gill membrane. The number of pinnules of the gill varies from twelve to thirty pairs. They alternate and often begin with a tubercle, so that the rachis appears tuberculate. In some animals the gill is regenerating. The genital apertures lie in the middle of the body or slightly anteriorly. According to their state of contraction or eversion they are flat, small and round, with or without a flap. The male atrium is partly everted and the tip of the cuticular penis is projected in about twenty of the present specimens (Figs 5C, E). In an animal of 10 mm the tip of the cuticular penis was well developed and stuck out of the male aperture.

The radular teeth are bicuspid except for about six of the outermost ones.

From the ampulla (Fig. 5A–B) the thin common genital duct (o), divides into male (e) and female (f) ducts. The latter recurves backward along the common duct. It is much wider initially, forming a ciliated serial spermatocyst. Vayssière (1901: 49) thought this was a caecum of the common duct, from which the efferent duct went out. Farther outward the female duct, which functions as both oviduct and insemination duct, is rather wide and has a high ciliated epithelium. The narrow efferent duct is surrounded by a ball of fine branching prostatic gland tubules (q). As it leaves these tubules, it widens and loops around the male atrium, entering the narrow penial sac (s) and traversing the retractor muscle (r) for up to 7 mm. It then turns outward and reaches the fundus of the atrium (a). The length of the efferent duct varies considerably along the retractor muscle and within the atrium. If the penial sac remains intact during preparation, the aspect of the duct is as in Bergh's (1897: pl. 7 fig. 14) figure. When it is torn, it appears like Vayssière's (1901, fig. 249) figure. In its descending course the efferent duct is separated into a sheath (h) and the cuticular penis proper (p). This is a stylet of 0,12 mm diameter at its base, narrowing to 0,08 mm in diameter. Its length varies from 1,9 to 6 mm. The chitinous penis enters the atrium through a small papilla. The penial cuticle is rough on the outer side (Fig. 5D). Vayssière's (1901, fig. 25D) figure of the tip of the penis corresponds to our observations, but we cannot confirm his interpretation of its muscular nature.

The oviduct begins with a winding spermatocyst and continues to widen slowly to the stalk of the spermatheca (t). The vagina (v) is short and wide and receives the outlets of the albumen and mucous glands. The atrium is generally long and narrow when inverted, or short and wide when partially everted. Its epithelium contains transverse bands of glandular cells.

Discussion

Both Bergh and Vayssière studied specimens from Verrill's original material, but neither of them observed the cuticular stylet. They figured only the tip of the penis (Bergh 1897, pl. 7 (fig. 27); Vayssière 1901, fig. 250). Vayssière considered the penis of his specimens (30–40 mm alive, 14–16 mm preserved) incompletely developed. In the present material a preserved animal 7,5 mm in length had a well-developed cuticular penial stylet. The inward loop of the effer-

ent duct in Bergh's (1897, pl. 7 (fig. 14)) figure is held together by the penial sac, while in Vayssière's figure it is loose.

Bergh (1897: 28–30, figs 16–18) described *Pleurobranchaea meckelii* var. *occidentalis* from Martinique. Marcus, Ev. & Marcus (1967a: 45–48, fig. 55A–C) identified specimens from Florida with Bergh's form and raised this to species level due to the different penial sac. Marcus & Marcus figured the penis in its sheath (their fig. 55C). Comparing this and the present animals with *P. tarda* in Vayssière's figure 249, the authors did not find any difference and consider *P. occidentalis* as a synonym of *P. tarda*.

Pleurobranchaea capensis was described from two specimens from the Cape of Good Hope collected in 1829. Vayssière (1901: 46–49, figs 232–237) described the inward loop of the efferent duct as being similar to that of *P. tarda*. However, it did not have a loop around the atrium (Fig. 5A).

Bergh (1907: 30) identified twenty-seven of his South African specimens as *P. capensis* Vayssière, with the 'vas deferens much shorter than in *P. meckelii*'. One specimen Bergh (1907: 32, pl. 11 (figs 1–8)) called *P. capensis* var., because it had a 'much longer vas deferens than represented by Vayssière (fig. 232)'. The present ample material showed a high variability of the length of the male duct. The extremes corresponded to those described for *P. tarda* and *P. capensis*. Hence *P. capensis* Vayssière must be considered as a junior synonym of *P. tarda* Verrill.

Pleurobranchaea brockii Bergh, 1897

Figs 6–8

Pleurobranchillus brockii Bergh, 1892: 28, *nom. nud.*

Pleurobranchaea brockii Bergh, 1897: 41–46, pl. 4 (figs 8–17). Vayssière 1901: 62–69, figs 255–260. ? Farran, 1905: 355, pl. 5 (figs 24–28). White, 1948: 20. Macnae, 1962: 178. Lin Guangyu & Tchang Si, 1965: 275, pl. 1 (fig. 3).

Pleurobranchaea brockii var. Bergh, 1897: 46–47, pl. 7 (figs 33–38), pl. 8 (fig. 1).

Pleurobranchaea gemini Macnae, 1962: 178, fig. 7a–c.

Material

South African Museum: SAM–A29866, two specimens, no locality; SAM–A30078, one specimen, no locality; holotype *P. gemini*, SAM–A35234, Inhaca Island, collected by W. Macnae, 18 July 1958; paratype *P. gemini*, SAM–A35236, Inhaca, collected by W. Macnae, 19 July 1958; SAM–A35237, two specimens and egg mass, Inhaca Island, collected by W. Macnae, December 1967.

Distribution

Japan to South Africa.

Description

The preserved specimens are 38–110 mm long. The notum is smooth or macillate. The colour, when preserved, is a net of black pigment around more or

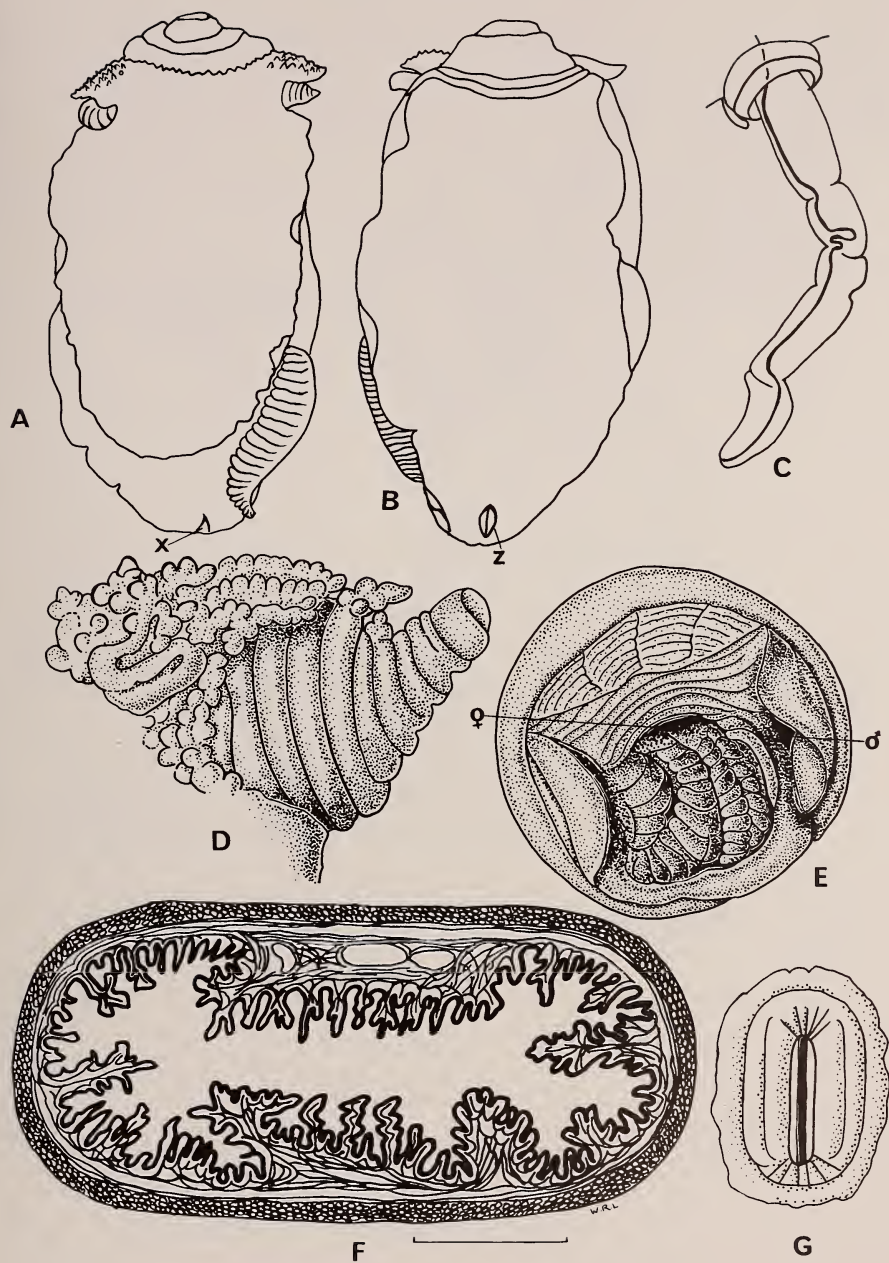


Fig. 6. *Pleurobranchaea brockii* Bergh, 1897. A. Dorsal view of preserved specimen. B. Ventral view. C. Extruded penis. D. Tentacle and rhinophore. E. Gonopore. F. Transverse section of vagina, scale 0,5 mm. G. Anterior of pharynx with borders of jaws.

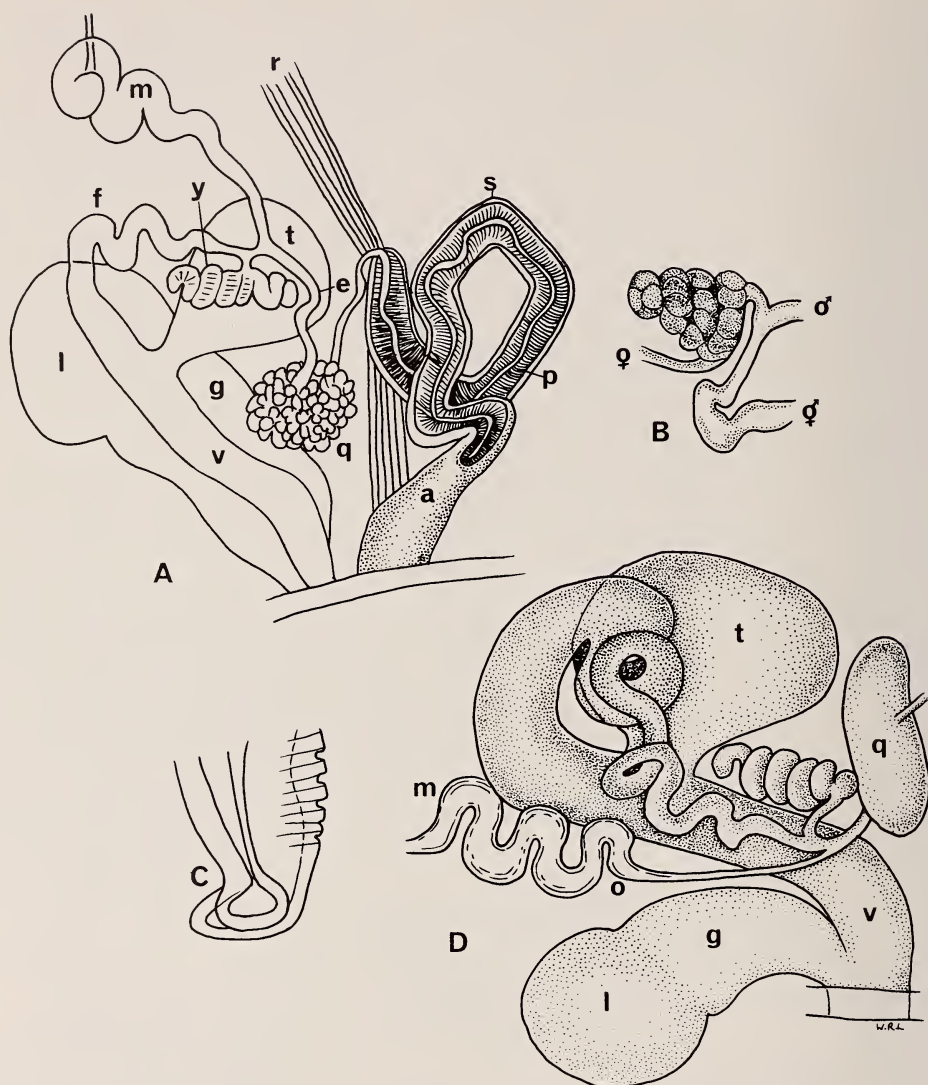


Fig. 7. *Pleurobranchaea brockii* Bergh, 1897. A. Diagram of reproductive organs of specimen SAM-A30078. B. Spermatocyst. C. Tip of contracted penis. D. Female organs.

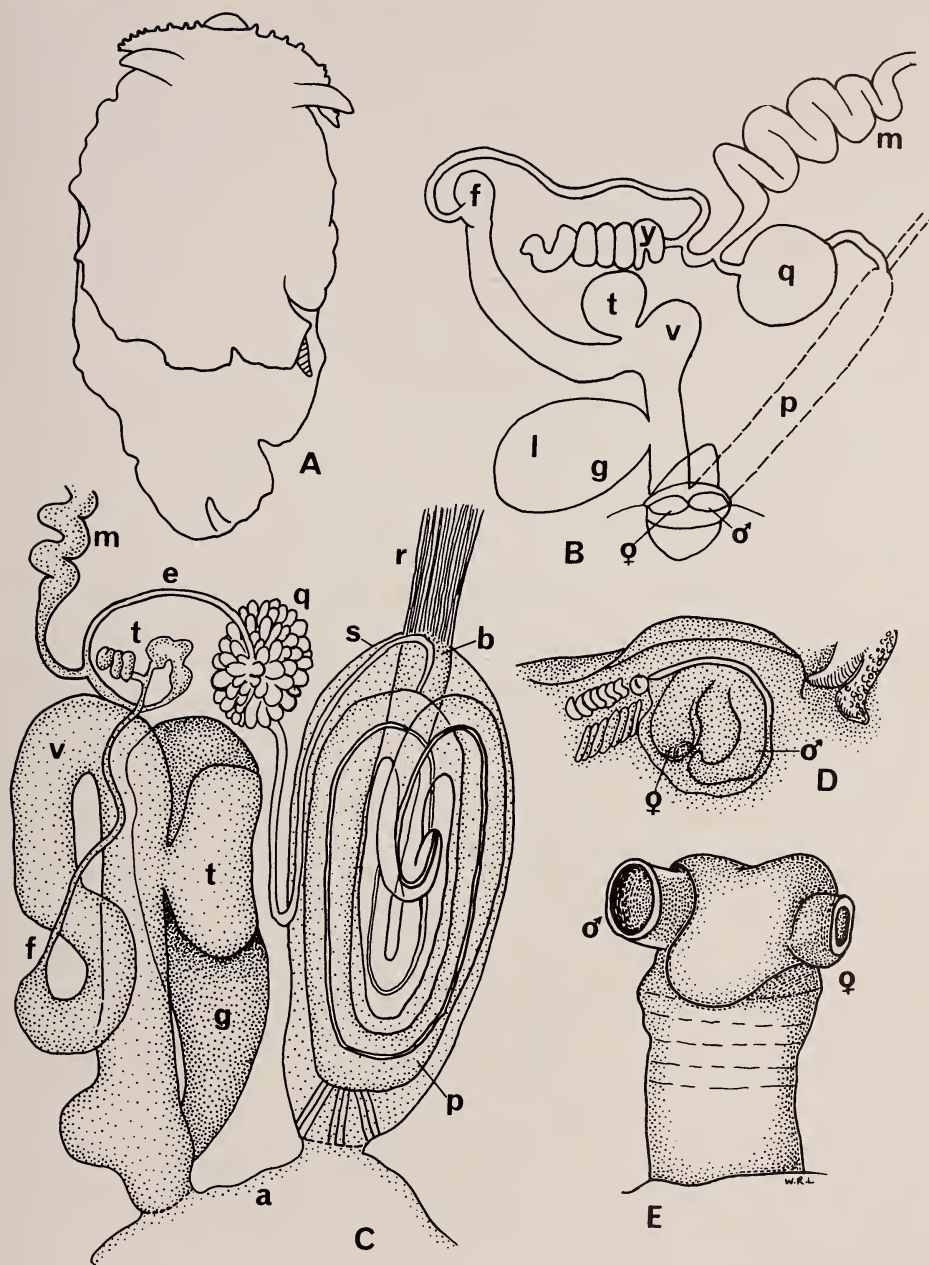


Fig. 8. *Pleurobranchaea brockii* Bergh, 1897, paratype of *P. gemini*. A. Dorsal view of preserved specimen. B-C. Reproductive organs. D. Gonopore with a partially everted atrium. E. Everted male and female pores.

less regular light circles or big blotches, which contain mamillae. Pigment is also present on the upper side of the foot. The notal border is free around its entire surface. There are sixteen papillae on the border of the oral veil arranged in two rows. The anterior side of the tentacles is thickly papillate in the South African Museum specimens (Fig. 6A, D). In those from Inhaca there are fewer tubercles (Fig. 8A). The rhinophores are set in deep sinuses between the tentacles and notum. The foot projects further posteriorly in the specimens from Inhaca (Fig. 8A), but this may be an artifact of preservation. A spur and a foot gland are present or absent. The gill rachis is narrow; the base of the 30–40 pairs of pinnae may bear a knob.

The jaw plates have a straight anterior border (Fig. 6G). Their denticles are present or absent and are irregular in number and size. The radular formula is $40-48 \times 65-90.0.65-90$. The teeth are bicuspid but the outermost laterals are sometimes unicuspid. Vayssi re (1901, fig. 260) mentioned and figured a rachidian tooth, but said it was atrophied and often lost or absent. It seems to be the fused first laterals. The radula of the holotype specimen of *P. gemini* is missing. Those of the paratypes are, like that of *P. brockii*, without a rachidian tooth.

The male duct passes through the prostate (Fig. 7A) and enters the narrow penial sac (s). There it forms a strong muscular, non-cuticularized penis (p). The retractor muscle inserts on the middle of the dorsum and traverses the sac to the atrium. In a contracted state the penis is curled (Fig. 8C). When extruded it is up to 4 cm long (Fig. 6C). The shape of the atrium could not be determined. When everted it is a wide and very thin sac (Fig. 8D), and when completely extruded the male and female pores open on its innermost stronger part (Fig. 8E). The gonopore is surrounded by a circular fold with some flaps.

The oviduct, after separating from the common duct, has a swollen part (Bergh 1897, pl. 4 (fig. 8)), that sometimes forms a small caecum lying at the beginning of the spermatocyst (Fig. 7A). In most specimens the latter forms a longer caecum with three to five spirals, but rarely it is only a widening with epithelial pouches in the duct. The duct narrows into several whorls and then widens suddenly as the vagina. The vagina is long (Bergh 1897: 46) and its epithelium is divided into many folds (Fig. 6F). Farther outwards the spermathecal pouch opens into the vagina. The vagina joins the albumen and mucous glands. It often has an ectal widening on one side.

The holotype of *P. gemini* had previously been opened only for the radula. The female organs were intact (Macnae 1962, fig. 7c). The male organ was examined for comparison. It corresponds to Bergh's (1897) figure. The spawn is a tall convoluted ribbon 13 mm wide, like that of *P. californica*.

Discussion

The descriptions of *P. brockii* and *P. gemini* are similar, and Macnae's distinctive characters are not convincing: *P. brockii* 'is characterized by a mamelonnated mantle' while the 'smooth, not mamillated surface' of *P. gemini* is not

mentioned in the description, only in the comparison. In some of Macnae's paratypes which we observed the mantle was smooth, in others mamillate.

In all available specimens the sixteen velar papillae are set in two rows. In the South African Museum specimens SAM-A29866 and SAM-A30078, the tentacles are thickly covered with papillae (Fig. 6D), while in Macnae's animals there are only a few. This merely represents intraspecific variation. Bergh found no trace of rachidian teeth in the radula of *P. brockii*. In Macnae's (1962: 178) specimen of *P. brockii* they were 'very deciduous and all had fallen off . . . and were found in the debris at the bottom of the watch glass'. In *P. gemini* they were not mentioned. Macnae's figure shows very long primary cusps and the secondary cusp inserting near the base, but he (1962: 180) noted that they were 'without the basal prominence on the inner edge'. The teeth of the paratypes of *P. gemini* that were examined are like those of *P. brockii*. The radulae of ten specimens were studied and a basal prominence was found in all specimens. It is sometimes not visible when the teeth are tilted and this fact may explain why Macnae did not notice the prominence in the holotype.

The 'long and worm-like penis' of *P. gemini* described by Macnae (1962: 180) was not figured. Bergh (1897, pl. 4 (fig. 8)) and Vayssi re (1901, fig. 256) illustrated the large, soft, non-cuticular penis of *P. brockii*. A second caecum on the outer oviduct of *P. gemini*, to which the spermatheca is attached (Fig. 8B), is not recognizable in Bergh's figure of *P. brockii* nor in the dissected specimens from Inhaca. Based on the variability observed in Macnae's type material and the similarity of it to *P. brockii*, the two species are thought to be synonymous.

Pleurobranchaea agassizii Bergh, 1897

Fig. 9

Pleurobranchaea agassizii Bergh, 1897: 48, pl. 7 (figs 28–32). Marcus & Marcus, 1967a: 49, 51, fig. 56A–D.

Distribution

Straits of Florida; Great Bahama Bank, 262–620 m.

Description

Length up to 10 cm; radular formula $32 \times 98.0.98$. About seventeen of the outermost teeth lack the secondary denticle. The efferent duct (Fig. 9E) does not enter the penial sac but, where the retractor muscle is attached to it, it divides into a sheath and a muscular penis without cuticle. (After Marcus, Ev. & Marcus, 1967a).

Discussion

In Marcus & Marcus's (1967a: 49–51) description there were two errors. P. 51: the allosperm duct does not rise through the efferent duct but through the vagina and insemination duct, which is the outer oviduct. In figure 56D the ovi-

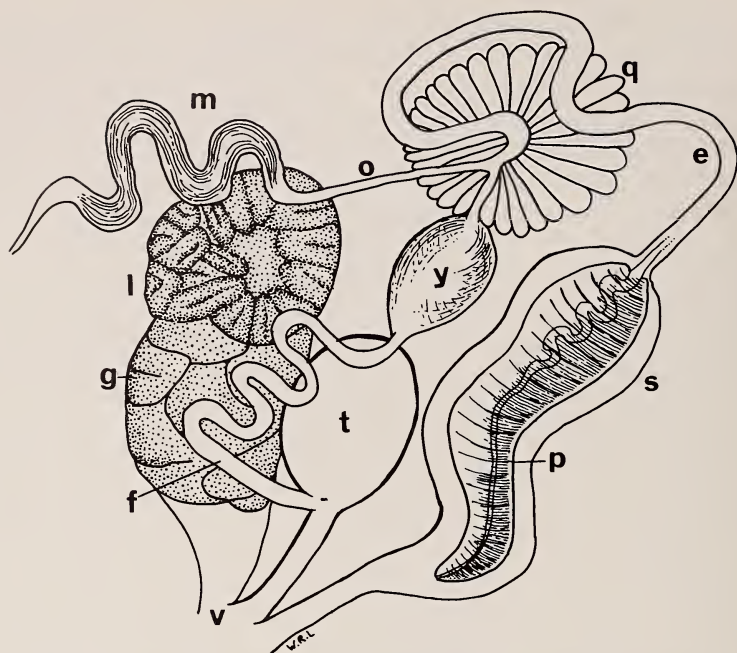


Fig. 9. *Pleurobranchaea agassizii* Bergh, 1897, Reproductive organs.

duct is shown entering the albumen gland; actually, it only passes near the female gland mass and continues to the vagina, where it receives the secretions of the albumen and mucous glands.

Pleurobranchaea inconspicua Bergh, 1897

Figs 1B, 10-11

Pleurobranchaea inconspicua Bergh, 1897: 49, pl. 8 (figs 2-10).

Pleurobranchaea hedgpethi Abbott, 1952: 1, pl. 1 (figs 1-8). Marcus & Marcus, 1959: 253, fig. 6. Marcus, Er., 1961: 141. Marcus & Marcus, 1967b: 200. Marcus & Marcus, 1969: 18. Nijssen-Meyer, 1965: 143, figs 1-3.

Pleurobranchaea gela Marcus & Marcus, 1966: 174, figs 35-37. Marcus & Marcus, 1968: 1336.

Material

About twenty-five specimens from 37°N to 5°N, 54°W to 86°W, 27-310 m; one specimen from Atlit, Israel.

Further distribution

From Cape Hatteras to Argentina; Texas; Ivory Coast to Nigeria.

Description

The preserved animals range from 11 to 55 mm in length and are in various states of contraction. Often the buccal mass is everted around the large

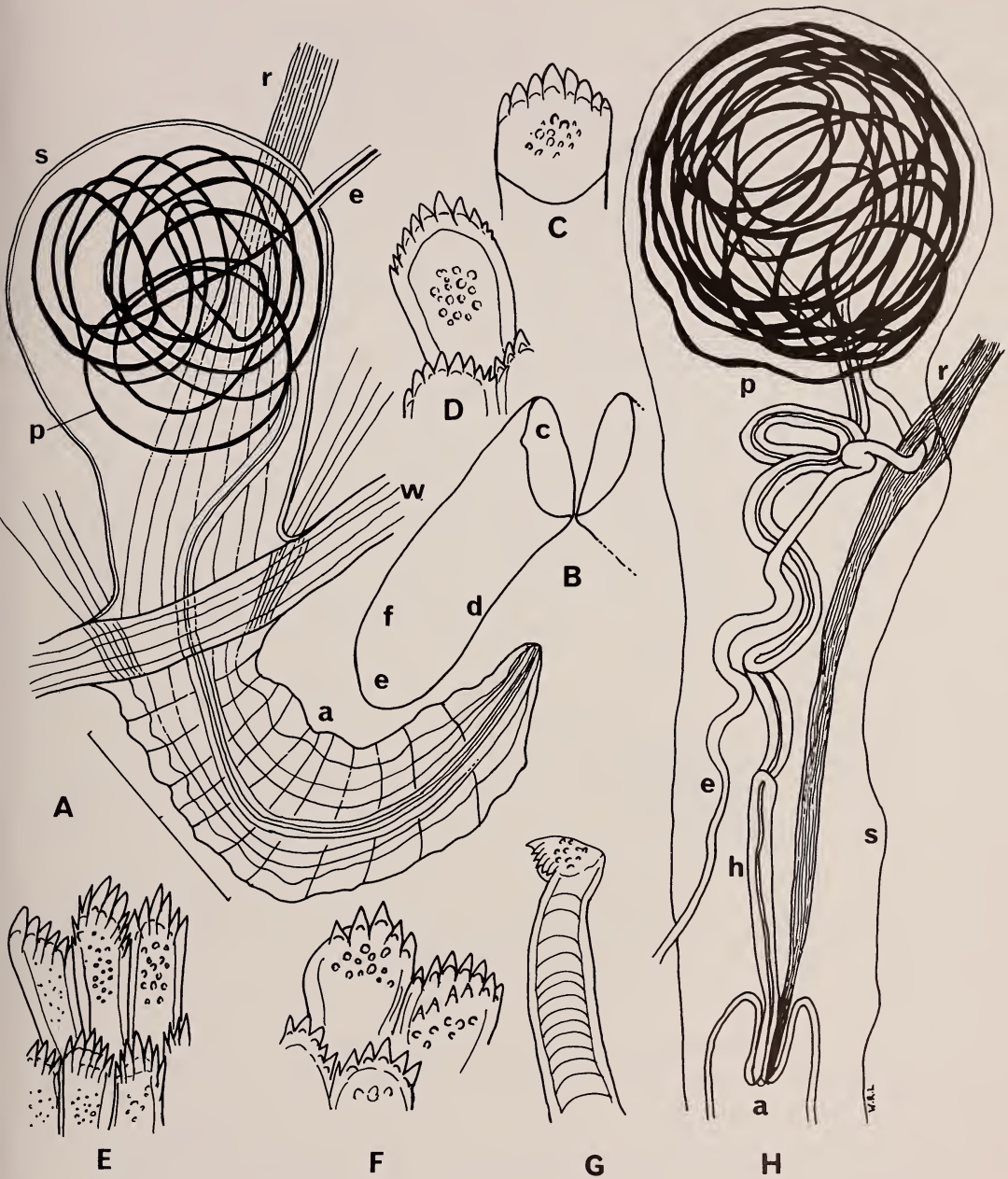


Fig. 10. *Pleurobranchaea inconspicua* Bergh, 1897. A. Everted penis, scale 2,0 mm. B. Jaws showing location of platelets in C-F. C-F. Platelets from various locations. G. Lateral view of platelet. H. Penis of specimen from Israel.

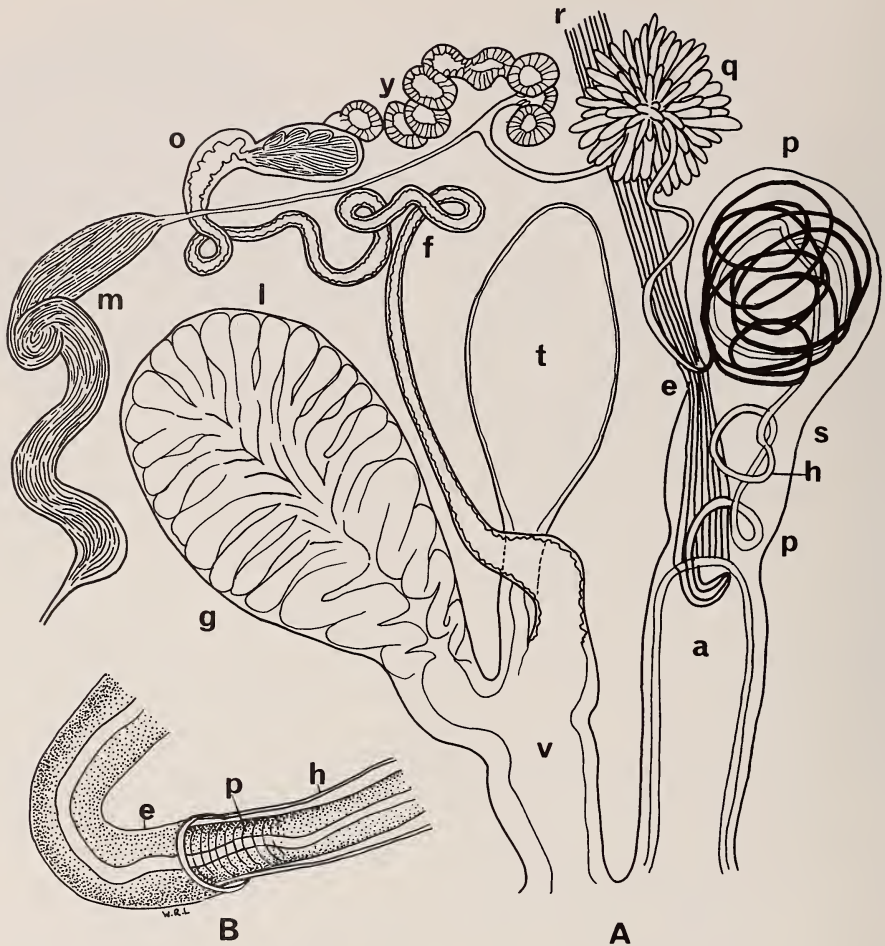


Fig. 11. *Pleurobranchaea inconspicua* Bergh, 1897. A. Diagram of reproductive organs. B. Root of penis and penis sheath.

projected pharynx. The anterior borders of the jaw plates are then visible, and sometimes even the radula. Also the male atrium can be everted (Fig. 10A), and the cuticular penial stylet may be observed. The notum is smooth or has some bosses separated by pigment, which is sometimes retained in these furrows.

The jaw plates of a 15 mm long animal were $4,6 \times 2$ mm. In a 26 mm specimen they were $5 \times 1,6$ mm. They are colourless in small specimens and light brown in the largest ones. The platelets are composed of columnar rodlets whose surface is often hexagonal. Their length varies according to their position in the jaw and with the size of the animal. The anterior border has a row of five

to fifteen denticles and often some knobs on the surface. These both can be lost in the anterior, oldest part of the jaw plate.

The radular formula is $32-40 \times 55-68.0.55-68$. The lateral teeth are bicuspid as in other species of *Pleurobranchaea*, largest in the middle of the half-row and smaller towards the outer border. Up to twenty outer teeth lack a secondary denticle.

The ovotestis and hermaphroditic duct are typical of the genus, as are the male duct and prostate (Fig. 11A). The male duct is 0,13 mm in diameter. Beyond where the male duct enters the penial sac, it is surrounded by a sheath (Fig. 11B). Its lumen is cuticularized and stiffens the duct so that it forms up to twenty roundish loops (Fig. 10H). This is the eversible penis proper, which may reach 14 mm in length when extended. It is ovoid in transverse view, and flattened on one side. Its lumen is circular or higher than broad (Fig. 1B). Ectally it gradually tapers to its tip. It is difficult to find the point where the penial sheath is separated from the penis proper, owing to the many loops of the efferent duct. Therefore it was not distinguished in the figures of the penial sac. The sheath is about 0,34–0,40 mm in diameter at its outer part. It ends forming a small papilla in the fundus of the male atrium. The papilla is up to 7 mm long and 2 mm wide. The entire male organ reaches 20 mm in length. The atrium can be everted for copulation (Fig. 10A) and the cuticular stylet projected. The smallest animal with a cuticular penis was 11 mm long. In material from 40°S, up to 20 mm long, specimens still did not have genital apertures (Marcus, Ev. & Marcus 1969: 20).

Discussion

Pleurobranchaea inconspicua, of which Bergh had a single specimen from Brazil (Sergipe), is identical in all its described characters with *P. hedgpethi* Abbott, 1952. Hence it is considered as a senior synonym of *P. hedgpethi*. The insemination ducts of *P. hedgpethi* (Marcus, Ev. & Marcus 1959, fig. 6) and *P. gela* (Marcus, Ev. & Marcus 1966, fig. 37) were figured differently. These differences appear to be a result of their state of contraction. Marcus, Ev. & Marcus (1967a: fig. 56) illustrated the insemination duct of *P. hedgpethi*. It has two vesicles as described for *P. gela*. In the present collection both forms occur. It is believed that *P. gela* is also a junior synonym of *P. inconspicua*.

Pleurobranchaea augusta sp. nov.

Figs 1C, 12

Type material

Holotype: United States National Museum 809995, West Africa (17°02'S 11°40'E), 54 m.

Etymology

From the Latin *augustus*, meaning venerable.

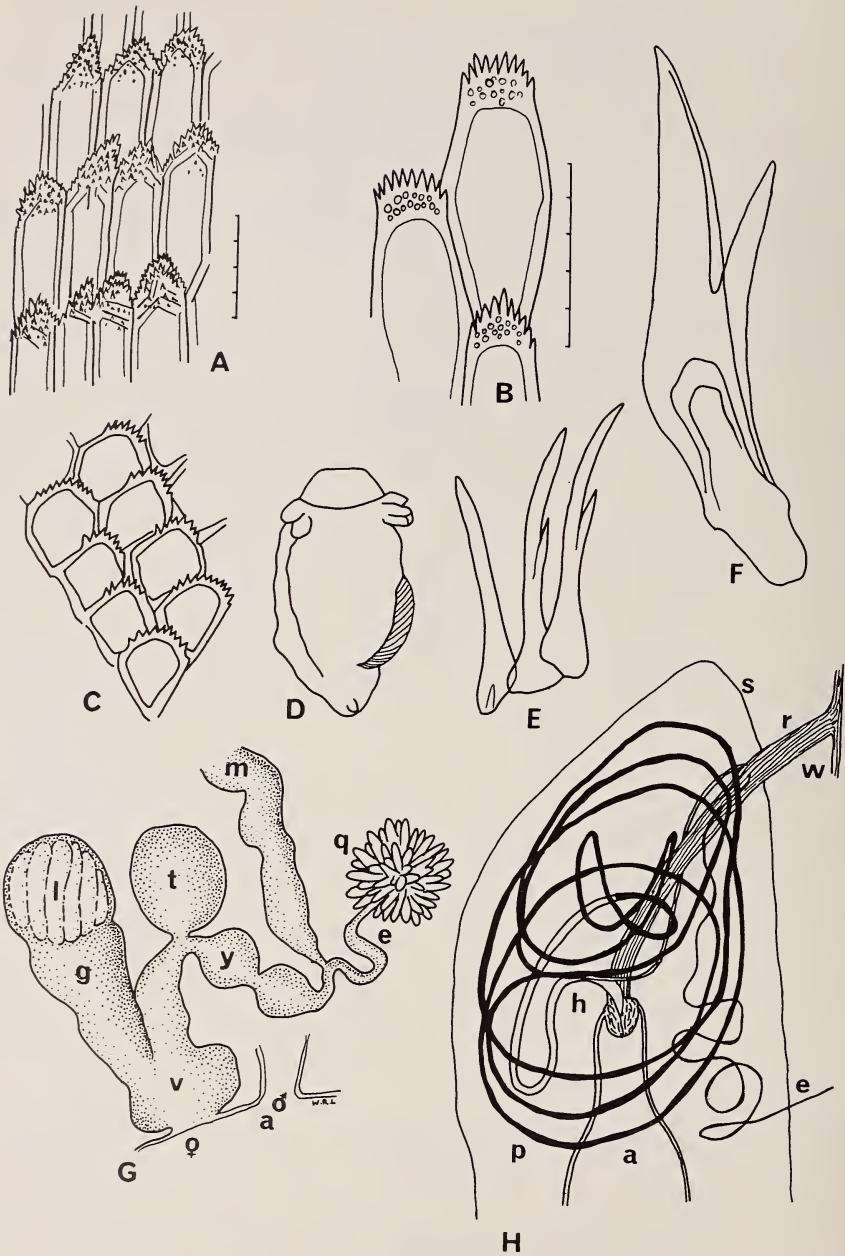


Fig. 12. *Pleurobranchaea augusta* sp. nov. A. Jaw platelets from middle of jaw, scale $40\ \mu\text{m}$. B. The same, from front of jaw, scale $50\ \mu\text{m}$. C. The same, from near border of jaw. D. Preserved animal. E. Outermost teeth. F. Radular tooth from middle of half-row. G. Female organs. H. Penial sac.

Description

The animal is 32 mm long, 20 mm broad, and 15 mm high, in the preserved state (Fig. 12D). It is colourless. The smooth notum forms an exhalant siphon over the tip of the gill. It is smaller than the foot. The foot has a tiny spur and a weak metapodial gland. The oral veil, tentacles and rhinophores are contracted. The gill has a smooth rachis with about twenty pinnae on either side. On the base of each of the pinnae there is a knob. Four-fifths of the length of the gill are adnate. The labial cuticle bears conical papillae. The platelets of the jaws vary in shape according to their position on the jaw. The central ones (Fig. 12B) have a long narrow surface with about ten denticles and some small tubercles behind them. The marginal platelets appear roundish with less numerous and shorter denticles (Fig. 12C). The radular formula is $40 \times 70.0.70$. The teeth are bicuspid (Fig. 12F) except for one or two of the outermost ones (Fig. 12E).

Ectally from the ampulla the hermaphroditic duct divides into the male efferent duct, and the oviduct (Fig. 12G). The former passes through the prostate and enters the thin, roundish penial sac in its middle. The efferent duct winds upward to the entrance of the retractor muscle which it penetrates (Fig. 12H). Later it divides, widening slightly, into the penial sheath and cuticular, stiff penis proper. Together the penis and its sheath form about six loops. In the present specimen the penis ends before the sheath opens into the atrium with a small papilla.

The penial cuticle is cylindrical with equally thick walls. It forms a sharp crest (Fig. 1C), which is visible in optical transverse section. This crest serves as the distinctive character separating *P. augusta* from *P. meckelii*, whose cuticle is more irregular. The globular spermatheca connects directly to the oviduct. The oviduct widens to form a short vagina into which the accessory female glands open. The female aperture is slightly posterior to the male aperture.

Discussion

The single specimen is similar to *P. meckelii*, but the shape of the penial stylet differs (Fig. 1C, 2B), and the vagina is longer in *P. meckelii* (Fig. 2C).

Pleurobranchaea bonnieae sp. nov.

Figs 1D, 13–14

Type material

Holotype: United States National Museum 809999, R. V. *Gerda*, Station G 1001, Florida (27°N, 80°W), 61 m, 21 May 1968, one dissected specimen and slides of the jaws, radula and genital organs.

Etymology

This species is named for Bonnie J. Gosliner.

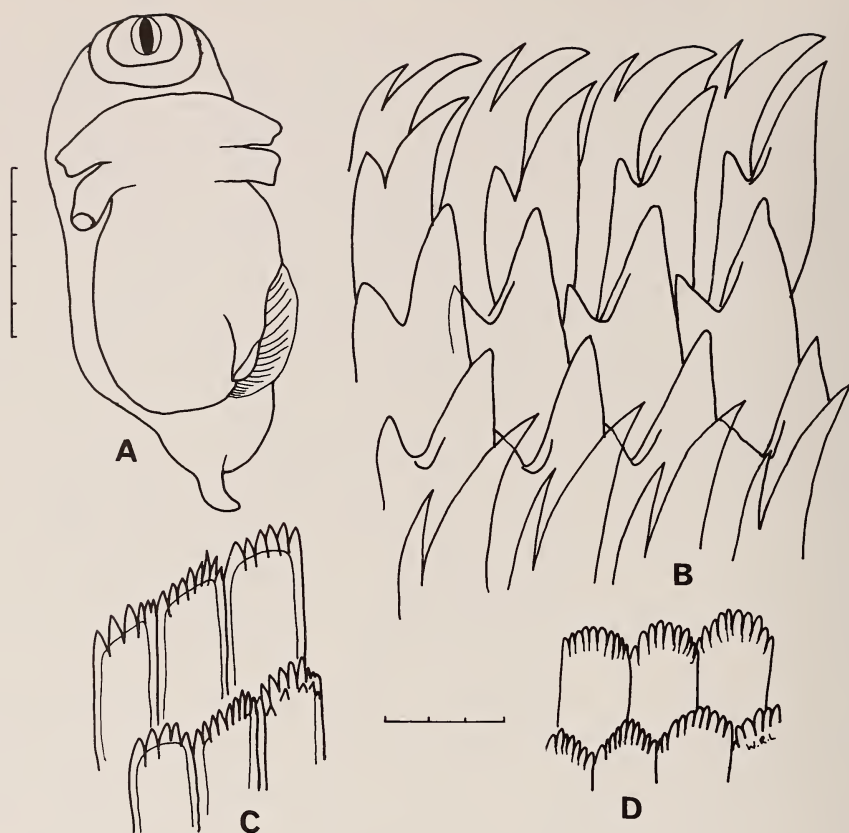


Fig. 13. *Pleurobranchaea bonnieae* sp. nov. A. Dorsal view of preserved animal, scale 5 mm. B. Abnormal rows of radula. C-D. Jaw platelets, scale 0,03 mm.

Description

The preserved animal is 15,5 mm long and 7 mm wide. Its mantle is slightly tuberculate, white, with bits of pigment retained on the rhinophores and the mantle. The foot is shorter than the notum anteriorly and longer posteriorly (Fig. 13A). The contracted oral veil is short and smooth. On the hind end of the foot is a prominent spur. A pedal gland was not observed. The gill rachis is smooth with about twenty pinnules on either side. The prebranchial gland opens at the beginning of the rachis. The genital apertures are retracted and there appears to be a single small pore without a flap.

The colourless jaw plates are 3 mm long and 1,5 mm wide. The platelets are up to 0,06 mm high. They are arranged in transverse, slightly slanting rows. Their surface is hexagonal. Near the anterior end they are about 0,034 by 0,018 mm (Fig. 13C), while posteriorly they are 0,046 by 0,018 mm (Fig. 13D).

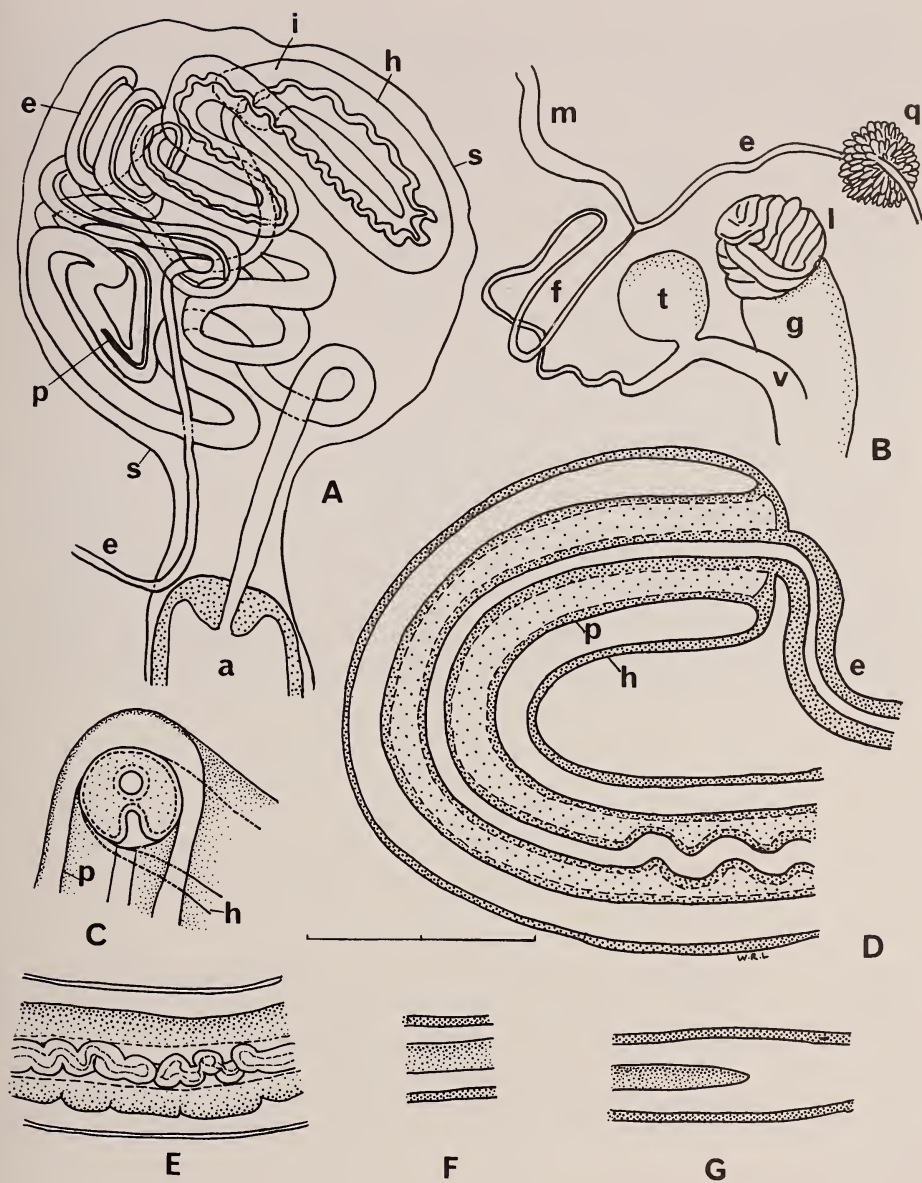


Fig. 14. *Pleurobranchaea bonnieae* sp. nov. A. Penial sac. B. Female organs. C. Optical transverse section of penis. D. Root of penis. E-G. Parts of penis in sheath, scale 0,2 mm.

The platelets bear nine to twelve denticles. The radula is 4,5 mm long and 2,4 mm wide. The largest of the light yellow, bicuspid teeth is 0,36 mm long. The formula is $35 \times 55.0.55$. About six of the outermost teeth are unicuspid. In the stomach was a 2 mm long aeolid nudibranch.

The reproductive organs were torn during preparation, but the male organ is complete. The globular penial sac is 1,2 mm in diameter, the atrium 1,6 mm long (Fig. 14A). A narrow efferent duct, 0,05 mm wide, traverses the penial sac and continues into the 0,14 mm wide penis proper. The penis is contained within a 0.25 mm wide penis sheath (Fig. 14D). For the first 1,4 mm of the looping penis the lumen is closely sinuous (Fig. 14E). Beyond this point the diameter of the penis diminishes to 0,07 mm while the sheath narrows to 0,12 mm in diameter (Fig. 14F). The 20 mm long organ is so tightly coiled that its further structure is not recognizable, except for the transverse section (Fig. 14C) and the tip of the penis (Fig. 14G). As a 0,082 mm wide tube the penis opens through a tiny papilla into the fundus of the atrium. On the basis of the structure of the penis and wide sheath around it we guess that the sheath is everted for copulation and the delicate, non-cuticular penis is protruded.

Discussion

While the single specimen may be juvenile, and the adult may have a cuticular penis, *P. bonnieae* can still be separated from all described members of the genus. *P. bonnieae* is most similar to *P. vayssierei* (Fig. 19B) and *P. notmec* (Fig. 18F), but differs by the wide base of the penis and in its shape in transverse section (Fig. 14C).

Pleurobranchaea bubala sp. nov.

Figs 15–17

Type material

Holotype: SAM-A35231, 1 specimen and egg mass, Buffels Bay at Cape Point, 10 m, collected by William R. Liltved, 4 October 1981.

Paratypes: SAM-A33966, one specimen, Simonstown harbour, Simon's Bay; SAM-A35232, 2 specimens, The Mill, Bakoven, Cape Peninsula, 20 m, collected by T. M. Gosliner, 16 September 1982.

Other material

SAM-A35233, 4 specimens, Inhaca, Mozambique, collected by W. Macnae.

Distribution

Specimens are known from the Atlantic coast of the Cape Peninsula to Inhaca, Mozambique.



Fig. 15. *Pleurobranchaea bubala* sp. nov., living animal.

Etymology

This species is named *bubala* after the genus *Bubalus*, the buffalo, as it is common at Buffels Bay, Cape Point.

Description

One living animal (Fig. 15) was 70 mm in length. The notum has a pattern of dark brown pigment and irregular whitish blotches. A well-preserved animal measured 50×35 mm. Its notum extends over the foot on both sides (Fig. 16A–B). Posteriorly it gradually merges with the foot. The oral veil has a row of small tubercles. A spur is absent. A triangle of pedal glands was visible in one living specimen. The gill has a smooth rachis with twenty-six pinnae alternating on either side.

The hexagonal jaw platelets have four to fourteen denticles, rarely more than ten. The radula formula is $35 \times 100.0.100$; 20–30 of the outer laterals do not have a secondary cusp (Fig. 16D).

The genital apertures are protruded and have a slight flap on the hind border. The glandular tubes of the prostate are united, forming globular masses (Fig. 16G). The efferent duct between the prostate and penial sac is thick, 0.6 mm in diameter, its lumen is 0.2 mm in diameter. The penial sac (s)

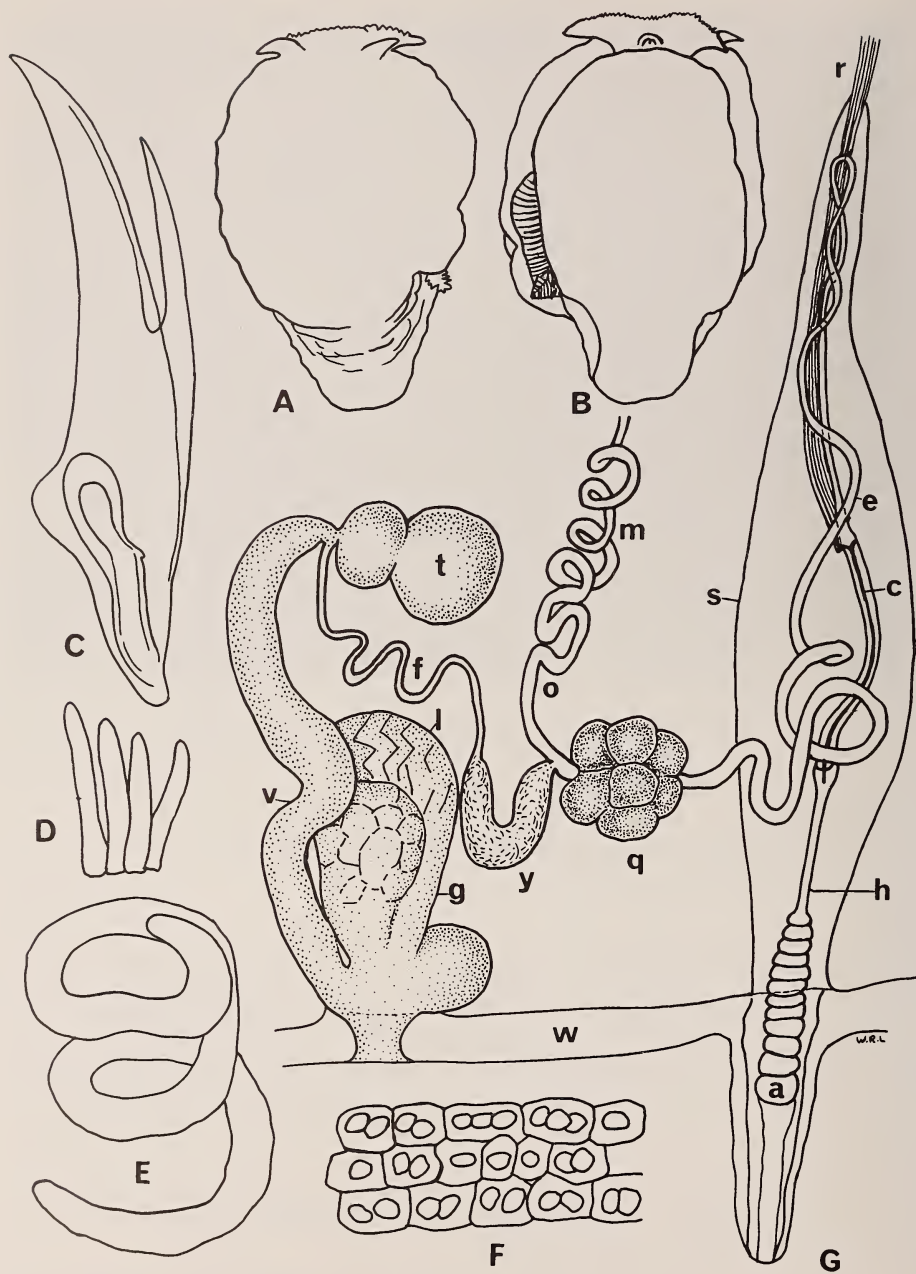


Fig. 16. *Pleurobranchaea bubala* sp. nov. A. Dorsal view of preserved animal. B. Ventral view of the same. C. Radular tooth from middle of half-row. D. Outermost teeth of row. E. Spawn. F. Eggs in spawn. G. Reproductive organs.



Fig. 17. *Pleurobranchaea bubala* sp. nov., egg mass.

accompanies the efferent duct (e) inward along the retractor muscle. It is wider in the middle than in *P. tarda*, but less globular than that of *P. inconspicua*. The cuticular stylet (c) is similar to that of *P. tarda* and about 5 mm in length. The atrium (a) is strongly muscular, 6–9 mm long.

The epithelium of the oviduct forms pouches, the spermatocyst (y). From the spermatocyst the oviduct narrows until it branches to the unstalked bilobed spermatheca (Fig. 16G). From this point the vagina (v) or insemination duct is much wider and has a high, folded epithelium. Near the female aperture it receives the accessory glands and forms a small caecum.

The egg mass (Figs 16E, 17) is a coiled tube of several irregular whorls. There are one to three eggs per capsule (Fig. 16F).

This species has been observed to feed on other opisthobranchs including members of its own species.

Discussion

The reproductive organs differ from the other species by the shape of the penial sac, the double spermatheca and the long glandular vagina. *P. bubala* is sympatric with *P. tarda* in South Africa and is distinguished by its larger size, abundant white blotches, elongate vagina, and the shape of the prostate (Figs 5A, 16G).

Pleurobranchaea notmec sp. nov.

Figs 1E–G, 18

Type material

Holotype: University of Israel, Department of Zoology 1005, eastern Mediterranean, off Turkey, 11–140 m.

Paratypes: University of Israel, Department of Zoology, two specimens, Haifa Bay; one specimen, Palmahim, 80 m; one specimen, No. 16399, northern Sinai, 45 m.

Etymology

The name refers to the fact that this species was originally identified as *P. meckelii*, from which it is distinct.

Description

The size of the preserved animals is from 12 to 40 mm long and 8 to 15 mm wide.

The surface of the mantle is slightly bossed, without tubercles.

The colour is not preserved, except some pigments in the furrows between the bosses. The animals are 'museum' brown. The notum is smaller than the foot. Its right border extends out over the gill. The anterior border of the notum forms the oral veil bearing a row of papillae. The sides of the veil are produced into pointed cephalic tentacles with split sides. The rhinophores are inserted between the tentacles and the lateral mantle border. They are as long as the tentacles, blunt, cylindrical, and rolled.

The anterior end of the foot is divided by a transverse furrow. The hind end bears a pointed dorsal spur. On the ventral side the pedal gland forms a longitudinal furrow.

The gill is about one-third of the body length and has twenty to thirty alternating pinnules on each side. Its anterior three-fourths to four-fifths are adnate. The anus is dorsal to the middle of the gill. The rachis is smooth.

The prebranchial glands open slightly anteriorly to the gill. A little more anteriorly are the genital apertures, united by a circular fold. Their shape varies according to contraction. A flap is absent. The large pharynx often protrudes from the mouth opening. The labial cuticle bears scattered papillae. The anterior border of the jaws appears whitish on the everted proboscis but is light brown when cleaned with potassium hydroxide. They are composed of columnar rodlets of variable shape, reaching 0,2 mm in height. The rodlets are polygonal, longer than wide. Ectally they measure about 0,05 mm in length and 0,04 mm in width. Posteriorly they are longer and narrower, the longest attaining 0,11 mm in length and 0,017 mm in width. Their frontal borders overlap and bear many small denticles, which are also present on the surface behind the border. The bases of the rodlets are more uniform in size. Anteriorly they are 0,05 by 0,03 mm; posteriorly 0,07 by 0,03 mm.

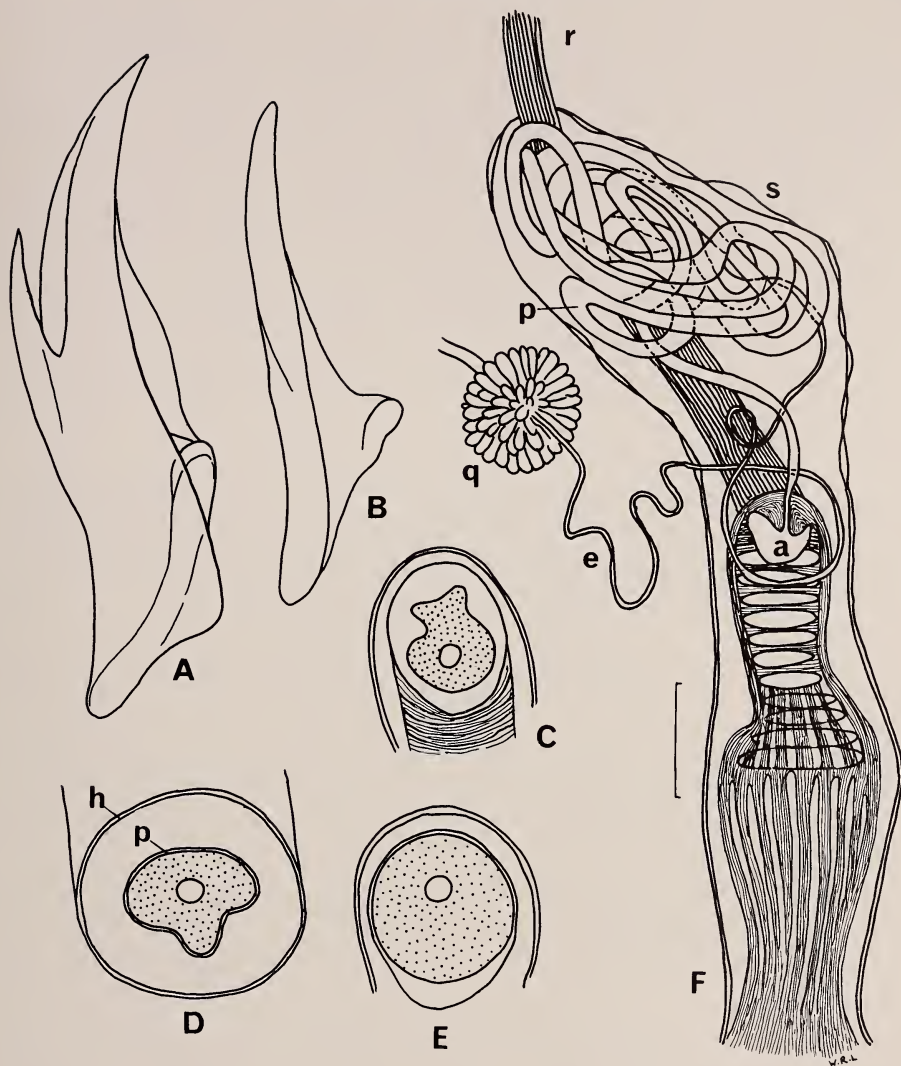


Fig. 18. *Pleurobranchaea notmec* sp. nov. A. Radular tooth from middle of half-row. B. Outer radular tooth. C-E. Optical sections of penis. F. Male reproductive organ, scale 0,3 mm.

The radula of the largest specimen is 16 mm long; each half is 5 mm broad. The formula is $50 \times 80.0.80$. The teeth have a small secondary cusp (Fig. 18A). In the middle of the half-row the longest teeth attain 0,65 mm in length and diminish gradually towards the outer edge. One to four outer teeth lack a secondary cusp (Fig. 18B).

The genital ducts are so compact that they could not be disentangled. The ovotestis follicles contain sperm or oocytes. The slender hermaphroditic duct widens into a long ampulla, narrows again, and divides into the male and female ducts. The male duct enters the round prostate (Fig. 18F, q) and emerges as a very thin efferent duct (e) which penetrates the penial sac (s) near its outer end. Inside the sac the penis is a long, winding tube, 0,17 mm in diameter. Its lumen is 0,10–0,14 mm in diameter. The penis has a very thin cuticle and is surrounded by a thin penial sheath (Fig. 18C–E), which must evidently be everted. After forming about six loops, the penis straightens and emerges in the male atrium as a small papilla (Fig. 18F). The atrium (a) is a wide, thick-walled sac that opens in front of the female pore.

It was not possible to follow the oviduct. It did not seem to have a spiralled spermatocyst.

Discussion

The present animals from Israel were originally identified as *Pleurobranchaea meckelii*. However, *P. meckelii* differs by its long whip-like, cuticular penial stylet. The single specimen of *P. vayssierei* (Fig. 19B) is also similar but lacks a cuticle around the efferent duct in the penial sheath.

Pleurobranchaea vayssierei sp. nov.

Fig. 19

Type material

Holotype: Museum National d'Histoire Naturelle, Paris, from Algiers, 1900, one specimen among Vayssière's specimens of *P. meckelii*, No. 52. (See p. 11.)

Etymology

The name refers to the fact that the unique specimen was found in the collection of Albert Vayssière.

Description

The preserved animal is 32 mm long, 11 mm broad and 10 mm high. The notum is as large as the foot, smooth and colourless. There is a tiny spur on the tip of the foot (Fig. 19A), and a weak metapodial gland on its underside. The oral veil is smooth, perhaps as a result of 82 years of preservation. The gill has a smooth rachis with twenty-six pinnae. The jaw plates (Fig. 19C) are broken. Their platelets are relatively broad (Fig. 19D). The platelets bear up to fifteen denticles, which disappeared after mounting them in glycerine. The radular formula is $35 \times 65.0.65$. The teeth are dark greyish and bicuspid (Fig. 19E). None are unicuspid on the outer border.

The male duct forms many loops in the tight transparent penial sac (Fig. 19B). A stylet is not recognizable. The single specimen was so fragile that the female organs could not be dissected completely. The spermatocyst is a slight

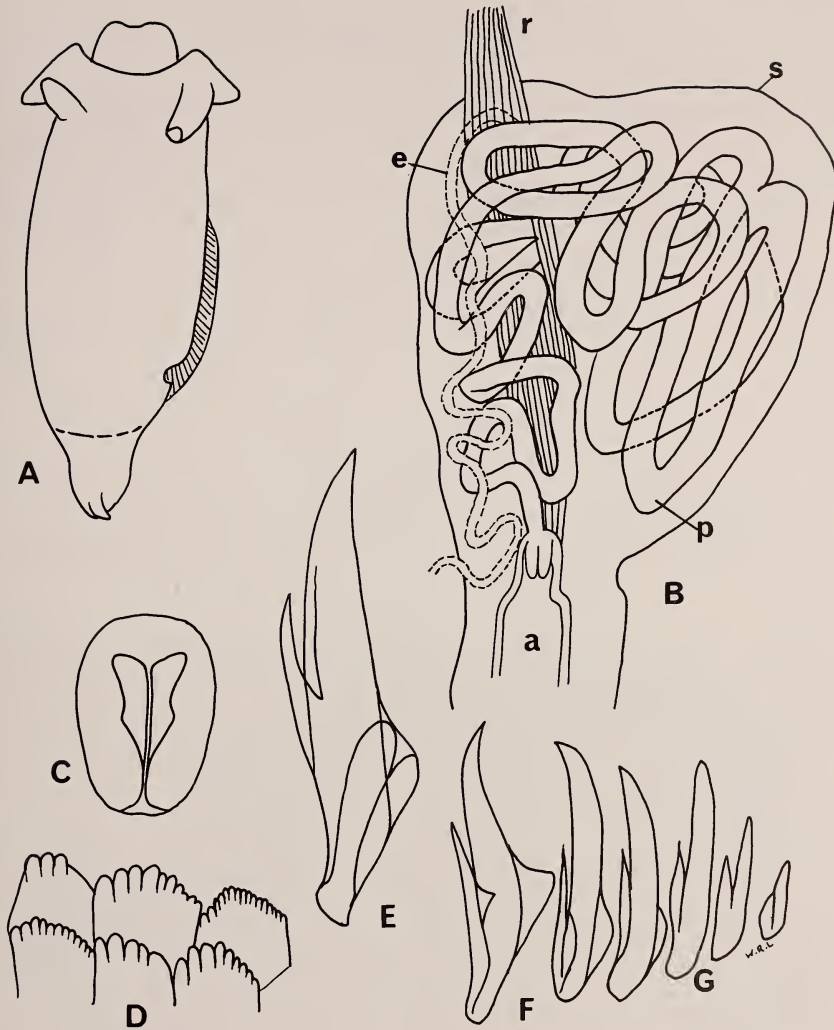


Fig. 19. *Pleurobranchaea vayssierei* sp. nov. A. Preserved specimen from Algiers. B. Penial sac. C. Anterior view of pharynx with jaws. D. Jaw platelets. E. Radular teeth from middle of half-row. F. Twenty-second outer tooth. G. Five outermost teeth.

widening of the oviduct, and the oviduct is continued into a long, rather narrow, ciliated vagina.

Discussion

The most similar species is *P. bonnieae* from Florida (Fig. 14A), which has an enlarged root of the penis. In *P. notmec* up to twenty teeth of the radula are unicuspid.

Pleurobranchaea (Macfarlandaea) subgen. nov.

Type species

Pleurobranchaea californica MacFarland, 1966.

Diagnosis

Pleurobranchaeidae with rudimentary secondary cusps on all radular teeth.
Pleurembolic penis with cuticular stylet.

Etymology

The subgeneric name honours the late Frank Mace MacFarland of Stanford University.

Pleurobranchaea (Macfarlandaea) californica MacFarland, 1966

Figs 20–22

Pleurobranchaea californica MacFarland, 1966: 94–101, pl. 15 (figs 16–28), pl. 17 (figs 1–17).
Chivers, 1967: 515–521.

Pleurobranchaea sp. Coan, 1964: 173.



Fig. 20. *Pleurobranchaea (Macfarlandaea) californica* MacFarland, 1966, living animal.

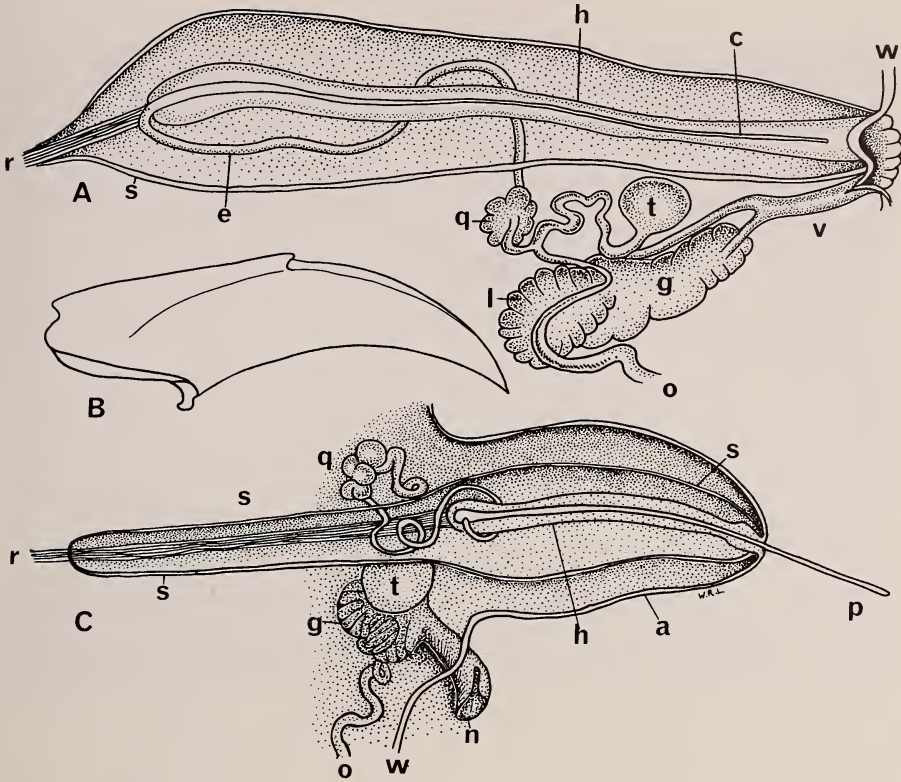


Fig. 21. *Pleurobranchaea (Macfarlandaea) californica* MacFarland, 1966 (after MacFarland 1966). A. Reproductive organs (retracted). B. Radular tooth. C. Reproductive organs with everted penis.

Distribution

California, from Klamath River to San Diego, 10–470 m.

Description

The living animal (Fig. 20) is brown with white blotches, up to 335 mm long. The rhinophores are typical of the family Pleurobranchaeidae. The jaw platelets are columnar with denticles. The radular formula of a 165 mm long animal is $52 \times 130\text{--}145.1.130\text{--}145$. All the lateral teeth have a rudimentary secondary cusp (MacFarland 1966: pl. 15 (figs 22–24)). The penis sac (= penis sheath, MacFarland 1966) is long (2 cm in an adult specimen) and not quite close around the penial sheath (= preputium, MacFarland 1966). The efferent duct accompanies the retractor muscle upwards and they enter the sheath together. Here the sheath separates from the whip-like muscular penis. The egg mass is a highly convoluted collar (Fig. 22).

Coan (1964: 173) observed that the species is carnivorous and cannibalistic.



Fig. 22. *Pleurobranchaea (Macfarlandaea) californica* MacFarland, 1966. Egg mass.

Euselenops Pilsbry, 1896

Pleurobranchaea (Euselenops) Pilsbry, 1896: 228. Thiele 1931: 419.

Neda Adams & Adams, 1854. *Non* Mulsant.

Oscaniopsis Bergh, 1897: 53. Vayssi  re, 1901: 6.

Type species

Pleurobranchus luniceps Cuvier, 1817.

Diagnosis

Notum much smaller than foot, penis papillate.

Euselenops luniceps (Cuvier, 1817)

Fig. 25D–G

Pleurobranchus luniceps Cuvier, 1817: 186.

Oscaniopsis semperi Bergh, 1897: 55, pl. 6 (figs 7–27).

Oscaniopsis compta Bergh, 1897: 58, pl. 8 (figs 11–27).

Oscaniopsis amboinei Vayssi  re, 1898: 9, fig. 27; 1901: 15, figs 190–204.

Non Oscaniopsis pleurobranchaeana Bergh, 1907: 35, pl. 4 (figs 16–21).

Oscaniopsis luniceps Vayssi  re, 1901: 15.

Euselenops luniceps O'Donoghue, 1929: 55, figs 65–74. Pruvot-Fol, 1933: 107. Burn, 1962: 131.

Lin Guangyu & Tchang-Si, 1965: 269, 275, fig. 4.

Distribution

Indo-Pacific: Hawaii, China, Hong Kong, Hainan, Japan, Philippines, Amboina, Queensland, Mauritius, Inhaca, South Africa, ?Red Sea.

Description

The length is up to 90 mm (Lin Guangyu & Tchang Si 1965) with the notum much smaller than the foot and its hind end forming a projecting tip. The radular teeth are unicuspid. The prostatic cells are contained in the efferent duct and the acrembolic penis is covered with soft cones.

Discussion

One 12 mm long specimen from Palmahim, Israel, had the outer aspect of *Euselenops* with a broad velum, small notum, large foot, and a notch in the hind end of the mantle. At first glance it seemed to be a *Euselenops* sp., but it was discovered that the radula was bicuspid, that the notal notch was the siphon of the gill, and that there was a large spur on the tip of the foot (Fig. 25B), indicating that it was a *Pleurobranchaea* sp. As the reproductive organs were not developed, the species could not be determined.

Pleurobranchella Thiele, 1925

Pleurobranchella Thiele, 1925: 283. Willan, 1977: 151.

Pleurobranchoides O'Donoghue, 1929: 62.

Pleurobranchaea (*Euselenops*) *Pleurobranchella* Thiele, 1931: 419.

Type species

Pleurobranchella nicobarica Thiele, 1925.

Diagnosis

Unicuspid species of Pleurobranchaeidae; notum covering foot on all sides; acrembolic penis with cuticular hooks.

Pleurobranchella nicobarica Thiele, 1925

Figs 23–24

Pleurobranchella nicobarica Thiele, 1925: 283, pl. 33 (figs 9–11).

Pleurobranchoides gilchristi O'Donoghue, 1929: 62, figs 75–85. Eales, 1937: 371.

Pleurobranchoides sp. Eales, 1938: 90, fig. 10.

Material

SAM-A33973, three specimens (105 mm, 115 mm, 150 mm long, preserved), Monte Belo, Mozambique, 400 m.

Distribution

Nicobares, Gulf of Aden, southern Africa, 220–269 m.

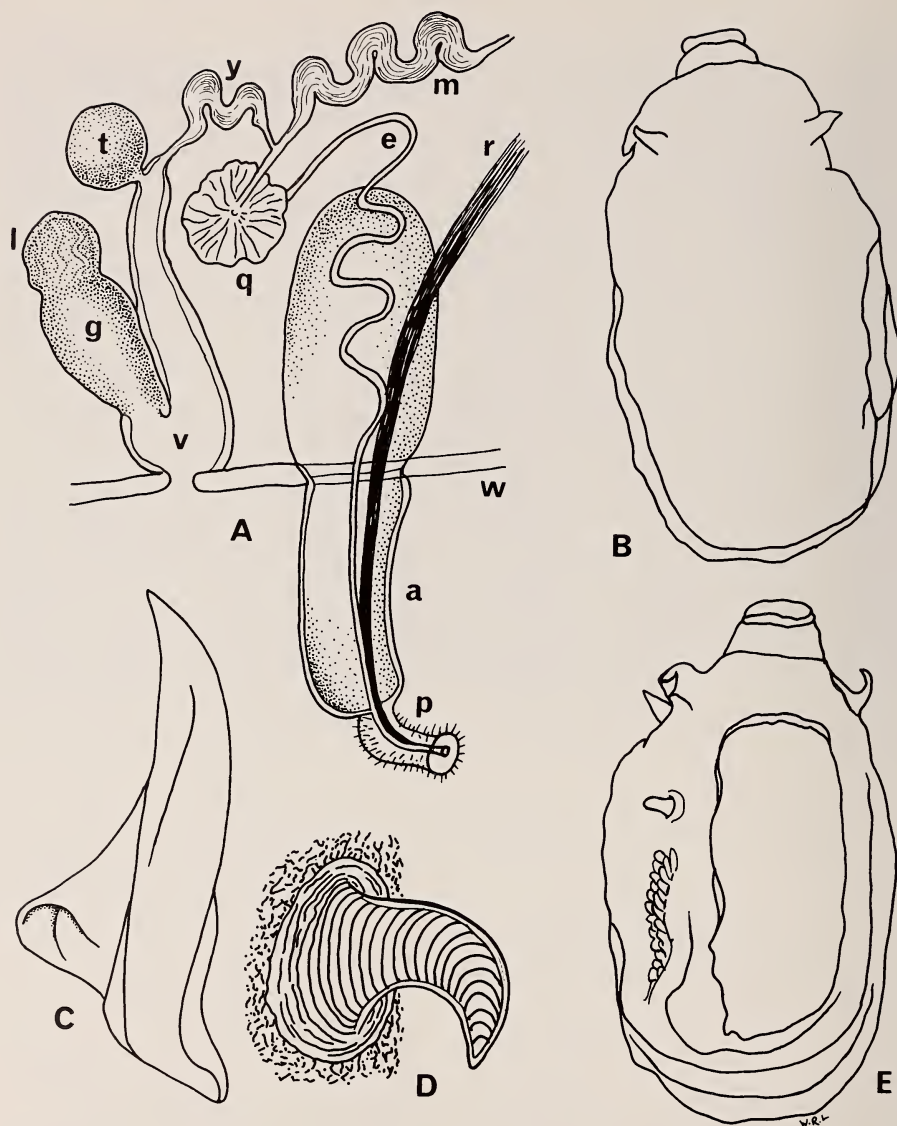


Fig. 23. *Pleurobranchella nicobarica* Thiele, 1925. A. Diagram of reproductive organs. B. Dorsal aspect. C. Radular tooth. D. Penial hook, scale 100 μ m. E. Ventral aspect.

Description

The large mantle extends far over the foot on all sides (Fig. 23E). The radular formula is $60 \times 133.0.133$. The extruded penis (Fig. 24B) consists of a wide everted atrium and a long cylindrical, slightly spiralled penis proper. Its concave

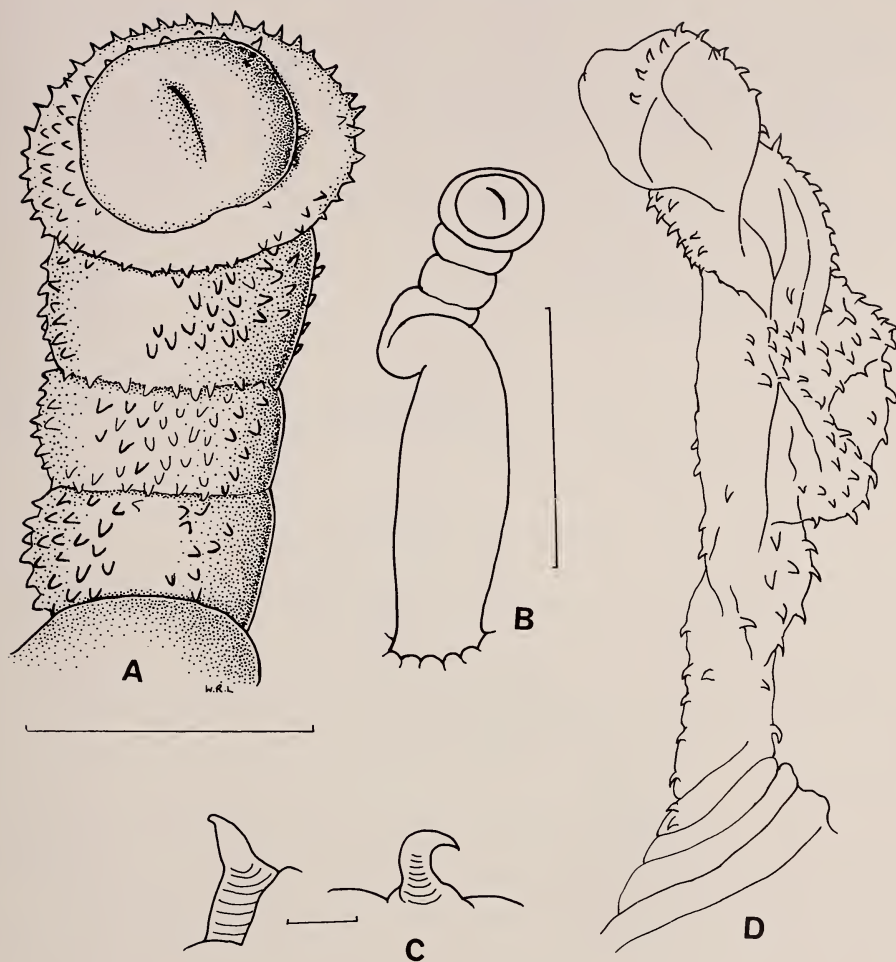


Fig. 24. *Pleurobranchella nicobarica* Thiele, 1925. A. Outer end of penis, scale 2,0 mm. B. Extruded penis, scale 5,0 mm. C. Penial hooks. D. Penis removed from retracted sac.

side is smooth; the convex side is covered with hook-shaped papillae (Fig. 24C–D). The extruded atrium is 30 mm long and 8 mm wide in the largest specimen. The penis proper is 7 by 2 mm in the largest specimen and 6 by 2,5 mm in the smallest.

Discussion

Though Thiele (1925) did not figure the penis of his *Pleurobranchella nicobarica*, his description is precise enough to identify the present specimens with his material. O'Donoghue gave only a short description of *Pleurobranchoides*

gilchristi, but it is considered sufficient to synonymize it with *Pleurobranchella nicobarica*.

Eales's (1938: 90, fig. 10) *Pleurobranchoides* sp. from the Gulf of Aden has a papillate penis and is certainly identical with *Pleurobranchella nicobarica*.

Koonsia Verrill, 1882

Koonsia Verrill, 1882: 545.

Type species

Koonsia obesa Verrill, 1882.

Remarks

Pilsbry (1896: 221) considered *Pleurobranchillus* Bergh, 1892, as a synonym of *Koonsia*, but Bergh (1897) transferred *Pleurobranchillus* to *Pleurobranchaea*, as did Willan (1977: 153).

Koonsia obesa Verrill, 1882

Fig. 25C

Koonsia obesa Verrill, 1882: 545, *partim*; 1884: pl. 28 (fig. 7); 1885: 571, fig. 107. Abbott, 1974: 349, fig. 2046.

Distribution

Western Atlantic, ?Martha's Vineyard: ?Delaware Bay, 400–560 m.

Discussion

Verrill (1882) included two distinct species in his original description. In his description of the genus Verrill (1882: 545) stated that 'the back is overhanging both on the sides and posteriorly, and there is a distinct mantle edge all around'. This agrees with the species description that 'the mantle forms a ring along the lateral and posterior borders'; it does not correspond to the figure of *Koonsia obesa* but to his distinct paratypes, which have been examined (see *P. confusa*). He stated that 'the foot is narrower', as in the paratype. In the generic diagnosis Verrill stated that 'the verge is armed with small hooks, but the spicule, present in *Pleurobranchaea*, is not protruded in any of our specimens of *Koonsia*, if present'. He neglected to mention this in the species description, but noted of *Pleurobranchaea tarda* 'the verge . . . with rows of minute recurved hooks near the end, and terminated by a slender, curved spicule' (Verrill 1882: 546).

The paratypes without hooks seen by Bergh (1897), Vayssi re (1901), and the authors (Fig. 3) are quite different from Verrill's figure (1885: 107). They also differ from his figures of *P. tarda* (1882, pl. 58 (fig. 6); 1885, fig. 105), which possess a stylet, but lack hooks.

As Bergh (1897: 33) did not find penial hooks in the paratype specimen of '*Koonsia obesa*' from the original locality, he rejected *Koonsia* and placed *K. obesa* in *Pleurobranchaea*. The authors believe that the distinct penial spines

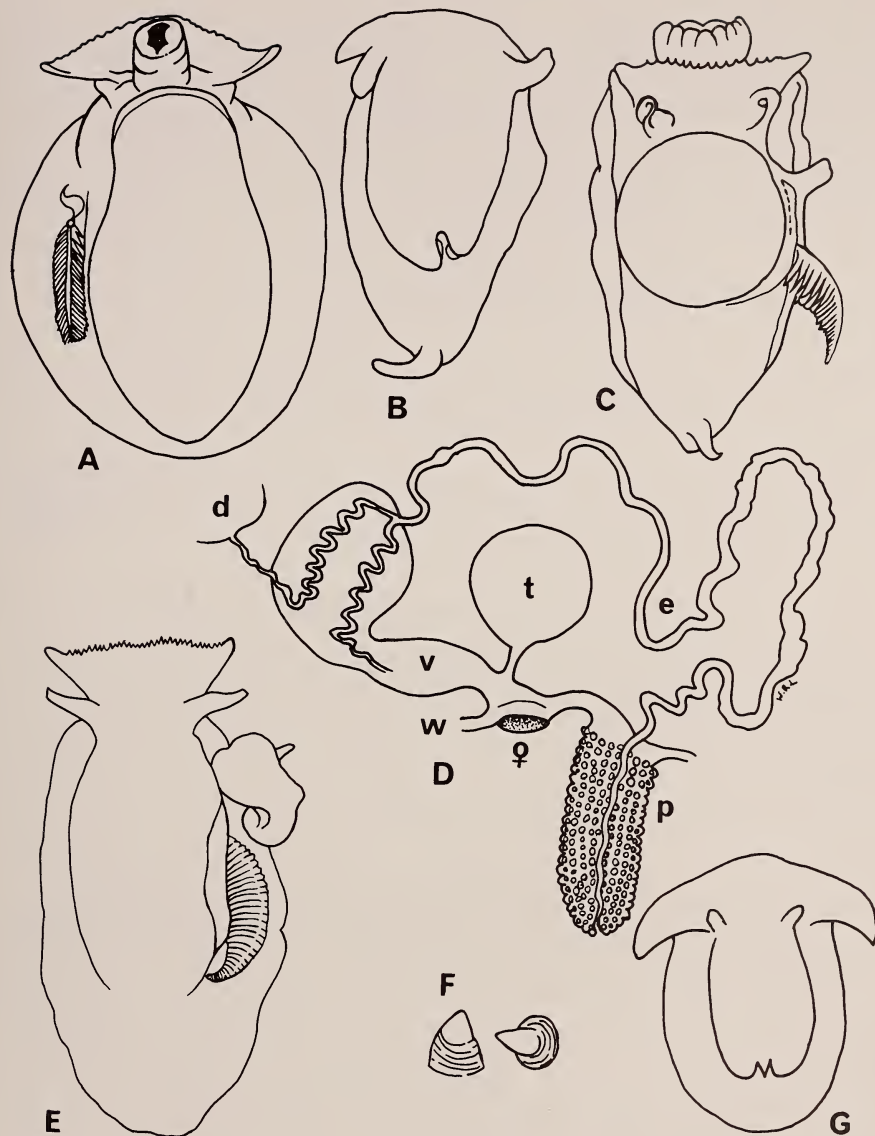


Fig. 25. A. *Gigantonotum album* Lin Guangyu & Tchang Si, 1965, preserved specimen (after Lin Guangyu & Tchang Si 1965). B. Juvenile *Pleurobranchaea* sp. from Israel. C. *Koonsia obesa* Verrill, 1882, holotype (after Verrill 1882). D. *Euselenops luniceps* (Cuvier, 1817) reproductive system (after Vayssi re 1901). E. *Pleurobranchaea maculata* (Quoy & Gaimard, 1832), preserved specimen (after Baba 1937). F-G. *Euselenops luniceps*. F. Penial papillae (after Bergh 1897). G. Whole animal (after Lin Guangyu & Tchang Si 1965).

described by Verrill indicate that his type material actually represents two species and therefore name the paratype examined *Pleurobranchaea confusa*. If the slender species (Fig. 25C) is found again, its generic placement depends upon whether the radula is unicuspid or bicuspid. Until such time it is preferred to maintain *Koonsia* as a distinct genus. *Pleurobranchella nicobarica* Thiele, 1925, *Euselenops luniceps* (Cuvier, 1817), and *Pleurobranchus hirasei* Baba, 1971, are the only other notaspideans known to possess an ornamented penis.

Gigantonotum Lin Guangyu & Tchang Si, 1965

Gigantonotum Lin Guangyu & Tchang Si, 1965: 270.

Type species

Gigantonotum album Lin Guangyu & Tchang Si, 1965.

Diagnosis

Pleurobranchaeid with a very wide mantle that covers the foot and the gill completely. Its borders are almost half as wide as the foot. Its underside bears nodules. The radula is unicuspid; its formula is $52 \times 144.1.144$.

Gigantonotum album Lin Guangyu & Tchang Si, 1965

Fig. 25A

Gigantonotum album Lin Guangyu and Tchang Si, 1965: 270, figs 5–6, pl. 1 (fig. 5d, v).
Pleurobranchella alba Willan, 1977: 153.

Distribution

South of Hainan Island, China Sea, 220 m.

Discussion

Lin Guangyu & Tchang Si (1965) compared their species with *Koonsia*, but stated that in *Gigantonotum* the foot is covered by the mantle, while it extends posteriorly for a considerable distance in *Koonsia*.

On the whole, *Gigantonotum* is similar to *Pleurobranchella* which, however, lacks a rachidian tooth. The geographic proximity makes a synonymy probable. Willan (1977: 151) synonymized *Gigantonotum* with *Pleurobranchella*, but considered only the incomplete previous descriptions. As long as the reproductive organs of *G. album* remain unknown it is preferable to consider *Gigantonotum* as a distinct but doubtful genus.

ZOOGEOGRAPHY OF THE PLEUROBRANCHAEIDAE

Only preliminary zoogeographical remarks can be made, owing to the fact that many records are based on unrecognizable, incompletely described, or unjustly synonymized species. In other cases information about the fauna of a region is incomplete. For example, Edmunds (1977) did not record any notaspideans from Ghana.

Five species of Pleurobranchaeidae have been recorded from the western Atlantic: *Pleurobranchaea tarda*, *P. agassizii*, *P. inconspicua*, *P. bonnieae*, and *Koonsia obesa*. Of these, *P. tarda* and *P. inconspicua* are more widespread. *P. tarda* is known from the eastern Atlantic coast of Africa from Ghana and from South Africa, where it extends into the Indian Ocean. *P. inconspicua* is also known from the Mediterranean and west Africa. *Pleurobranchaea meckelii*, *P. notmec* and *P. vayssierei* are known only from the Mediterranean, while *P. augusta* has been recorded only from west Africa. *P. bubala* is known from the Atlantic and Indian Ocean coasts of southern Africa.

Pleurobranchaea brockii and *Pleurobranchella nicobarica* are both known from the eastern and western Indian Ocean. *Euselenops luniceps* is widespread in the Indo-Pacific where it has been recorded from Hawaii to South Africa. Other species known from the Indo-Pacific region—*Pleurobranchaea maculata* and *Gigantonotum album*—may be widespread but their ranges need to be established from reliable records.

Pleurobranchaea californica is restricted to the Pacific coast of North America.

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ABBREVIATIONS

a	atrium	n	female pore
b	base of penis	o	spermoviduct
c	penial stylet	p	penis
d	hermaphrodite duct	q	prostate
e	efferent duct	r	retractor muscle
f	oviduct	s	penial sac
g	mucous gland	t	spermatheca
h	penial sheath	v	vagina
i	root of penis	w	body wall
j	rhinophore	x	spur
k	gill	y	spermatocyst
l	albumen gland	z	foot gland
m	ampulla	♀	female gonopore
		♂	male gonopore